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NEW SERIES—VOLUME XXXV, PART IV

A CENSUS OF THE DETERMINABLE GENERA OF THE STEGOCEPHALIA

E. C. CASE

Professor Emeritus of Historical Geology
and Paleontology
University of Michigan

THE AMERICAN PHILOSOPHICAL SOCIETY
INDEPENDENCE SQUARE
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A CENSUS OF THE DETERMINABLE GENERA OF THE STEGOCEPHALIA

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INTRODUCTION

In an attempt to gather together and evaluate all published information upon the Stegocephalia the author has encountered so much difference of opinion regarding the interpretation of specimens, so much confusion in the taxonomy, and so much speculation and attempted phylogeny based on imperfect and inadequate material that it has seemed imperative to make some census which would eliminate the erroneous, the obsolete, and the indeterminate in material and theory, and to emphasize such agreements as now exist among various workers.[1] In so doing it became immediately apparent that the great majority of the specific names proposed were of no value beyond indicating certain definite specimens or providing for more exact reference. All use of specific names for other purposes has therefore been dropped and the census confined to genera and higher groups.

The material presented consists of descriptions, taxonomic placement and restorations of determinable material which embody the most commonly accepted current opinion. A defence of this procedure will be found in the succeeding pages. The author has no hope or expectation that his drastic elimination of indeterminate material or his conclusions will be acceptable to all workers, but it is necessary from time to time to review the accumulation of data in any scientific subject and the theories based upon the data. Such "stock taking" constitutes the machinery for rejecting outmoded theories and faulty observations and makes for a uniformity of opinion which is the basis for intelligent advance. Such procedure is notably necessary for the biological branches where the unstable character of organic material prevents or resists exact measurement and leaves much to the judgment of individual workers. The problem of species, for instance, has become so complicated that an exact definition of a species is no longer possible.

However complicated the matter of classification may become, from the use of simple morphological criteria to the use of intricate genetic composition, the remarks made by the late Doctor Williston will remain true.[2]

> The relative importance of all such characters in classification is, however, largely a matter of the classifier's personal opinion. No two persons see them from the same viewpoint and consequently no two persons whose opinions deserve consideration ever wholly agree as to the value of characters in classification. It is only in the gradual crystallization of opinions that stability finally results, and this crystallization is never complete. So long as

[1] Notable examples of the confusion resulting from difference of opinion in the interpretation of specimens and of relationships are Romer's and Steen's attempted revisions of the Stegocephalian faunae of Nova Scotia, Linton, Ohio, and Czechoslovakia.

[2] Williston, S. W., The problem of classification, in his *Osteology of the Reptilia*, 208, Harvard University Press, 1925.

science endures, new facts will be discovered to influence our opinions. Any system of classification, then, merely represents the present state of our knowledge and the concensus of the opinions of those best qualified to decide as to their value, more or less influenced by the classifiers' individual opinions. No classification will ever be perfect, for perfection postulates complete knowledge. Fortunately, however, the increase of knowledge affects less and less the major principles, and more and more subordinate details.

Taxonomy is inherently protean. Its boundary lines and definitions stand only until errors or intermediate forms are discovered and the often devious course of evolution correctly traced. One is tempted to enlarge upon the rather cynical topic—the part played by ignorance in classification. The significance of these remarks is especially borne in upon the worker who deals with large intervals of time and long evolutionary series of forms. If geological time could be divided into satisfactorily short intervals and a sufficiently accurate knowledge of the fauna and flora of each interval obtained, a classification of the life of such intervals at least approximately equal to that of the present could be made and from a synthesis of such classifications a general picture of evolution might be made. Such a consummation is so remotely possible that it is unworthy of consideration.

Unhappily the paleontologist, as a paleobiologist, has attempted, though with constant misgivings and with a full recognition of the inadequacy of his material, to carry over into the study of fossils the methods of the neobiologist. Perhaps this was the only possible approach but the limitations of fossil material do not permit the refinements of neobiological methods and many well-meant but ill-destined attempts have produced a lack of confidence in the results.

The attempt to use the biological unit, species, in paleontology has in many cases produced little more than confusion. In certain situations where many individuals were concentrated, as in coral reefs or in beds of other sedentary invertebrates, an approximation amounting to an analogy, nothing more, can be made to the recognition of units equivalent to the living species. The convenience in expression is more than out-weighed by the error introduced. It is obvious that the only criteria that can be applied in fossil forms are morphological differences of the hard parts which are almost invariably the only parts preserved. This is especially true for large forms, as vertebrate animals and plants, where the material is commonly incomplete and distorted by the accidents of preservation and burial. As Sir Thomas Browne has said in his Urn Burial, "Time hath so martyred the Record."

For the reasons cited above, the value of a species in paleontology from the biological standpoint must long remain debatable. Any definite and recognizable difference in form may be used to identify and correlate beds, but aside from aid to stratigraphy, the use of specific description for rare or imperfect specimens can do little more than call attention to an individual specimen. As one famous vertebrate paleontologist has recently said, "One can always describe a new species."

This brief discussion, which might be expanded indefinitely, will indicate why the author has rejected the species of the Stegocephalia as unusable in the majority of cases, and considered only the genera and larger groups; the few specific names that are mentioned serve only to identify certain specimens or serve as a more exact reference. A few quotations will show that the author is not alone in his lack of confidence in fossil species.

Williston (1918) in discussing Permian vertebrates says: "but species of these fossils are elusive and indistinguishable from the accidents of fossilization."

Steen (1937), after listing the changes in the skull of *Acanthostoma vorax* Crd., says:

> In addition to these growth-changes, the relation of the individual bones and their exposures on the outer surface of the skull are extremely variable; e.g., the relation of the postfrontal, postorbital, and supratemporal; the lachrymal and the extent to which it enters into the external nares. This type of variation, which exists in all Amphibian species, exposes the fallacy of creating new species on slight proportional differences and variations in the exposures of individual bones.

Romer (1839) brings evidence to show that all listed species of *Branchiosaurus* are a congeries of larval forms of various undetermined amphibians.

Hartmann-Weinberg (1939) says that the changes in the proportions of the skull of *Archegosaurus* are so great that "it would be more correct to assign all known remains of *Archegosaurus* to one species, *Archegosaurus decheni* Goldf."

Thevenin (1910) made similar remarks concerning the skull of *Actinodon*.

Bystrow and Efremov (1940), after discussing the changes in proportions of the skull of *Benthosuchus* with growth, say:

> There is no doubt that many isolated, and even serial findings, described as new genera and species, are age stages or individual variations. We ascribe particular importance to the possibility of errors in the description of fragmentary imperfect material, on which, unfortunately the greatest number of new genera and species are based, only overcharging [confusing by multiplication, E.C.C.] the clear idea of the fauna, without contributing essentially to the knowledge of it.

A detailed account of their presentation of the changes with growth, and of individual variations, will be found under the discussion of the genus *Benthosuchus*, page 375.

The author, in common with every biologist, is fully conscious that there must have been great numbers of species among extinct animals and plants; his reservation in the use of specific names in paleontology is

based solely on the uncertainty which must attend their recognition from the evidence furnished by fossil material.

The Stegocephalia, originally a clearly conceived and defined group, has suffered the usual fate of all taxonomic groups; increased knowledge has so blurred the boundaries that neither its content, its origin, nor its fate can longer be stated with unanimity of approval by those best fitted to pass judgment. Through the Ichthyostegalia it approaches indefinitely the Devonian Crossopterygian predecessors and through the genera *Seymouria* and *Kotlassia* it passes indefinitely into the Reptilia.

Ever since the appearance of Zittel's *Handbuch der Paleontologie*,[3] the development of the classification of the Stegocephalia has conformed closely to Williston's formula of a "crystallization of opinion" in "those best qualified to decide." With few exceptions, workers have accepted the structure of the vertebral column as the most dependable character in its classification. Few notable departures have been taken from this procedure. Säve-Söderberg (1932) suggested that the structure of the skull was more dependable in classification. Bystrow (1944) has rejected the evidence of the vertebrae in placing *Kotlassia* in the Stegocephalia. Romer (1939) revived previous suggestions that the Phyllospondyli were not a distinct group but a heterogeneous and misunderstood assemblage of larval forms. Romer's proposal, however, is not a departure from a classification based on the vertebral column. It has been shown that the character of the vertebrae in one group shades into that of another, and that other characters must be appealed to in order to bolster the identity of the various groups.

The Ichthyostegalia, Phyllospondyli, Lepospondyli, Temnospondyli, Stereospondyli, Adelospondyli, and possibly Seymouriamorpha are today accepted as well established and well defined members of a larger group, no matter what new names or what new taxonomic rank may be proposed from time to time. With relatively few exceptions, there is a general concensus of opinion as to the component minor groups and the generic content of all but the Phyllospondyli and the Lepospondyli. The lack of agreement concerning these is largely due to their less perfect preservation caused by the accidents of postmortem destruction and fossilization. It is likely that a better understanding of them will result from the discovery of better material or of some improvement in the methods of investigation than from the formulation of new theories however brilliant.

In attempting a review of the present status of opinion upon the Stegocephalia, reference to the Urodela, Anura, and Gymnophiona has been avoided except as they are mentioned in relation to the Stegocephalia. A large measure of attention has been given to the skull as that region has been the subject of most of the recent work. Discussion of the literature has been limited to that of recent writers, partly because the older literature has been repeatedly reviewed and partly because more recent workers have had the advantage of accumulated material and of improved methods of investigation. Even with these restrictions the amount of literature is rather formidable, ranging literally from A(bel to Z(ittel). Those whose work has been reviewed are Abel, Augusta, Branson, Broili, Bulman, Bystrow, Case, Credner, Efremov, Hartmann-Weinberg, Hay, Haughton, Huene, Jaekel, Kuhn, Kuzmin, Mehl, Moodie, Romer, Smith-Woodward, Steen, Shushkin, Watson, Whittard, Zittel.

A practically complete bibliography of the Stegocephalia will be found in the following:

Fossilium Catalogus I. Animalia. Berlin, Junk.

KUHN, Oskar. 1933. Labyrinthodontia. Pars 61.

—— 1938. Stegocephalia (Labyrinthodontiis exclusis). Urodela. Anura. Pars 84.

NOPSCA, F. v. 1926. Osteologia fossilium et recentium. Pars 27.

—— 1931. *Ibid.* Appendix. Pars 50.

HAY, O. P. 1902. Bibliography and catalogue of the fossil Vertebrata of North America. *Bull. U. S. Geol. Survey* 179.

—— 1929. Second bibliography and catalogue of the fossil vertebrates of North America. 2 v. *Carnegie Inst. Washington Pub.* 390.

CAMP, C. L., and V. L. VANDERHOOF. 1928–1933. Bibliography of fossil vertebrates. *Geol. Soc. Amer. Special Papers* 27.

CAMP, C. L., D. N. TAYLOR, and S. P. WELLES. 1934–1938. Bibliography of fossil vertebrates. *Geol. Soc. Amer. Special Papers* 42.

In all phylogenetic lines which have been studied from sufficiently ample material there have been discovered certain trends in evolution which are continuous through time and definitely progressive toward a culmination which may be survival or extinction. As these are seemingly independent of environmental influences they have been conveniently called nonadaptive. In contrast there are minor changes of a common pattern which appear sporadically in different groups and repetitively in the same group, which are more or less obviously related to spatial and ecological factors, and which are generally apparent in the minor taxonomic groups such as genera and families rather than in orders and higher. These have been called adaptive changes. There is, of course, difference of opinion as to which group should receive certain characters.

The Stegocephalia show three definite trends in evolution. From a probably common ancestral form and aquatic habit there is (*a*) a persistent aquatic life with a weaker skeleton, (*b*) change to a more terrestrial life with a stronger and better mechanically adjusted skeleton, and (*c*) a return from a more terrestrial life to an aquatic life with a secondarily weakened (chon-

[3] The part dealing with the Amphibia appeared in 1888.

drified) skeleton. The common fate in the three trends was extinction of the group.

The following changes, generally regarded as non-adaptive, have been more or less definitely traced in the accomplishment of the trends.

1. The change of the occipital condyle from single, concave, tripartite (composed of the basioccipital and the exoccipitals) to double, convex, bipartite (composed of the two exoccipitals).
2. Reduction in number of the dermal roofing bones of the skull from the many of the Crossopterygian ancestor to the standard number of the Stegocephalian skull, by loss or coössification of certain elements.
3. Migration of the external nares from an original ventral to a dorsal position in the skull.
4. Fixation of the cheek bones to the roof of the skull by suture, replacing an original spiracular cleft or loose attachment.
5. Persistance and increasing dominance of the parasphenoid, finally replacing the basioccipital and basisphenoid as a ventral support of the skull—or increasing importance of the basioccipital and basisphenoid with reduction of the parasphenoid.
6. Increase in size of the interpterygoid vacuities with increase in size of the cultriform process of the parasphenoid.
7. Progressive chondrification of the bones of the brain-case in certain phylogenetic lines.
8. Perforation of the wall of the otic capsule by the fenestra ovalis.
9. Reduction in number of the bones in the mandible.
10. Progressive strengthening of the pelvis until the pubis is ossified.
11. Progressive change in the pectoral girdle.
12. Progressive development of the vertebrae until intermediate forms between the Embolomeri and the Rhachitomi, and between the Rachitomi and the Stereospondyli existed.

These non-adaptive changes appear in one or more of the three trends of evolution cited above. The same thing occurs more than once, as the progressive chondrification of the bones of the brain-case which is most strikingly developed in the Triassic Stereospondyli but appears at a much earlier date, the Carboniferous, in the Phyllospondyli, marking an at least unexpected specialization in a geologically and phylogenetically older group. This occurrence is termed precocious, indicating its unexpectedly early appearance.

The adaptive changes which appear once and again in the three trend lines form most of the generic and familial distinctions. The main ones are:

1. Number and form of the teeth.
2. Development and form of the cornua and otic notches.
3. Shape of the skull; largely due to the varying proportions of the bones which appear in practically the same pattern and the same number in all but the Adelospondyli.
4. Size and position of the orbits.
5. Degree of development of sensory canals.
6. Form of the body as related to the habits.
7. Presence or absence of dermal armor.

DISCUSSION OF NON-ADAPTIVE CHARACTERS

1. The single tripartite occipital condyle is a primitive character in the sense that it is an inherited character from an ancestral form. It exists in the Ichthyostegalia and the Lower Carboniferous (Westphalian) Embolomeri, and occurs sporadically in the Phyllospondyli (*Eugyrinus*). The loss of this character by the reduction of the basioccipital and the development of the exoccipitals undoubtedly accompanied the development of the tetrapodus habit and the increasing flexibility of the vertebral column, as the growth of ability to breathe air directly permitted greater variety of motion in progression and capture of prey. The persistence of this distinctly piscine character in the early Amphibia and its presence in both the Loxommidae and the Anthracosauridae, if these families were as different in their trends and fate as Säve-Söderberg believes, make it one of the critical characters in the evolution of the Stegocephalia.

2. The reduction in number of the bones in the roof of the skull from that of the Crossopterygian ancestor to the number common to most of the Stegocephalia is well established. Whatever terminology may be used, the number and relation of the bones and their relation to the sensory canals is extraordinarily stable when once fixed. Despite this fixed trend, the Carboniferous and Permian Adelospondyli and the ancestors of the modern Amphibia, whatever they were, early departed from the orderly path and entered upon a seemingly lawless course which makes it impossible to trace their origin with any certainty. Numerous efforts to do so have proved unconvincing; the latest is by Watson (1940) who makes a plausible effort to derive the Anura from the Phyllospondyli.

3. The migration of the external nares from a ventral to a dorsal position has been accepted by all as a significant step in the development of air-breathing. This change preceded somewhat the change in the occipital condyle and the alteration in form and position of the septo-maxillary (called the anterior antorbital by Säve-Söderberg). This bone moved from anterior to the orbit to a place immediately behind the naris and lost the sculpture of a surface bone, taking on the smooth condition of a deep seated one. Possible traces of this migration can be seen in forms other than the Ichthyostegalia, in the position of the nares

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far down on the side of the snout in *Orthosauriscus* and *Diplovertebron* (*Gephyrostegus*).

4. The ligamentous attachment of the cheek bones to those of the skull roof in the Loxommids is regarded as the last trace of the spiracular cleft present in the Crossopterygia. The closure of the fissure must have been early as it is already accomplished and the bones joined by suture in the Ichthyostegalia and the Anthracosauridae. The persistence of the loose attachment in one group and its loss in others forms the basis of Säve-Söderberg's contention that the two branches of the lower Carboniferous Embolomeri had already started on widely divergent courses. For a further account of this matter see the discussion of kineticism in the Stegocephalia below.

5. The development of the parasphenoid until it became one of the main elements of strength in the amphibian skull took place coincidentally with the secondary chondrification of the basicranial elements of the neurocranium. As the basioccipital and the basisphenoid became weakened, the parasphenoid took over their function. This trend in certain of the Stegocephalia is opposed to a trend in others in which the parasphenoid was weakened and the basicranial elements retained their importance, leading to the Reptilia.

6. The increase in size of the interpterygoid vacuities accompanied the increase in importance of the parasphenoid. The skull of the ancestral fish was kinetic and such rigidity as was present was due to the broad pterygoid plates closely approximated and united by suture at the anterior ends. This structure was directly inherited by the Ichthyostegalia and the early Embolomeri, but as the strength of the palate was shifted to the parasphenoid and the maxillary bones the pterygoids became narrower and the vacuities enlarged. It is noteworthy that as the maxillaries became stronger the function of grasping food was also shifted, and that with development of strong maxillary teeth the abundant teeth of the palatal surface gradually disappeared in most of the Amphibia.

With the development of rigid attachment of the cheek bones to the roof of the skull and development of the parasphenoid with loss of the basipterygoid processes for movable articulation with the pterygoids, the original kineticism of the Stegocephalian skull was lost in large measure. The succession of events originally suggested by Versluys has been traced by Dreverman (1920), Watson (1926), Pfannenstiel (1932), and Kuzmin (1938). Pfannenstiel recognized the presence of the meso-, meta-, and amphikineticism of Versluys in the Stegocephalian skull and added a fourth, pleurokineticism, in the loose attachment of the cheek bones to those of the roof of the skull. He traced the closure of the spiracular cleft, still open in *Eugyrinus*, and, as he thinks, in *Archegosaurus*, and the persistence of the structure in the loose attachment marked by the suture between the squamosal and the supratemporal-intertemporal bones. As this suture persists even after a firm interlocking of the bones is established he regards its presence as indicating ancestral kineticism. The perforate temporal region in *Cacops*, *Trematops*, and *Cyclotosaurus* he regards as due to partial bridging of the spiracular cleft by processes from the bones on either side. He believed that kineticism of this type might occur in any of the Stegocephalia except the Stereospondyli, in which it is entirely lost.

Kuzmin agreed in general with Pfannenstiel but asserted that pleurokineticism could still be detected in the Lower Triassic Stereospondyl *Rasaurus*. He gave the following table showing the type of kineticism which occurred in the various genera.

I. Complete Kineticism of the Skull

Articulations: basipterygoid, paroticotabular, squamosotabular

Paleogyrinus	Embolomeri	Carboniferous

II. Incomplete Kineticism of the Skull (*a*)

Articulations: basipterygoid and paroticotabular.

Orthosaurus	Embolomeri	Carboniferous

II. Incomplete Kineticism of the Skull (*b*)

Articulations: basipterygoid and squamosotabular.

Pholidogaster	Embolomeri	Carboniferous
Archegosaurus	Rhachitomi	Permian

III. Partial Kineticism of the Skull (*a*)

Squamosotabular articulation

Melanerpeton	Phyllospondyli	Carboniferous
Cricotus	Embolomeri	Carboniferous
Pteroplax	Embolomeri	Carboniferous
Ricnodon	Lepospondyli	Carboniferous
Rasaurus	Stereospondyli	L. Triassic

III. Partial Kineticism of the Skull (*b*)

Basipterygoid articulation

Ichthyostega	? Embolomeri	U. Devonian
Melosaurus	Rhachitomi	U. Permian
Dwinasaurus	Rhachitomi	U. Permian

How generally the work of Pfannenstiel and Kuzmin will be accepted remains to be seen. All authors from the time of Versluys have recognized some forms of kineticism in the Stegocephalian skull, occurring sporadically and most obvious in the relation of the basipterygoid processes to the pterygoids. Probably metakineticism persisted the longest. The loss of kineticism has been attributed to changing food habits and activities but is rather obviously a part of a long continued non-adaptive trend.

7. The progressive chondrification of the brain case has been described by various authors and is accepted by all. It is generally considered that it was due to the return to an aquatic life after the development of terrestrial habits and characters. The occurrence of pronounced chondrification in the genus *Trimerorhachis* is difficult to explain for though it is

one of the most striking examples there is no evidence of a more terrestrial ancestor.

8. The reduction of the number of bones in the mandible seems to be a definite trend in all of the Stegocephalia. It is largely in the reduction of the coronoid bones from three to one. All of these bones were crowded with small teeth but with the development of a strong dentition on the dentary the small teeth were lost.

9. The imperforate pit in the otic capsule of the Lower Carboniferous Embolomeri is understandable as the last stage before the development of the *fenestra ovalis*. It probably occurred coincidentally with the development of air breathing, marking the change of the ear from a receptor of water-borne sound waves to one for receiving air-borne waves. We have no knowledge of this region in the Ichthyostegalia but would expect it to be the same as in the older Embolomeri.

ADAPTIVE CHANGES

Most of the characters considered as adaptive are directly related to habits and environment. The same character may occur at different phylogenetic stages of the same line or in different lines. Undoubtedly there were many characters of this kind which are less obviously adaptive and cannot be explained satisfactorily. One of these is the development of the cornua. Originally the cornua were associated with the attachment of the skull to the shoulder girdle, but as this was lost they took over the function of support of the tympanic membrane. In some genera, as *Diceratosaurus* and *Diplocaulus* the enormous development can only be regarded as an exaggerated growth of unknown function. This is a case where a single character has had three successive functions.

COMPARATIVE TABLE OF CLASSIFICATIONS

The schemes of classification presented in table 1 continue from those given by Moodie in 1916. They include all that have been given in comprehensive publications, with the exception of that given by Jaekel (1922) which departs so far from the general concensus of opinion that it cannot be reconciled with the others. The sequence of publication has been disregarded where necessary to bring similar groups as nearly in line as possible to facilitate comparison.

The most important point affecting the classification of the Stegocephalia is the discovery of intermediate forms, showing transitional types of the vertebrae which cut across the long accepted boundaries of the main groups. How these groups shall be treated has not yet been established by usage. Säve-Söderberg (1935) speaks of the "so-called" Embolomeri and Rhachitomi, and Efremov (1937) used the term Neorhachitomi for forms intermediate between the Rhachitomi and Stereospondyli, but these groups are, from their very nature, impossible to contain within definite boundaries of classification. Säve-Söderberg says (1935) that the separation of the Rhachitomi and Stereospondyli is quite arbitrary and of no systematic value. "The fact seems to be that there is a general evolutionary trend toward a simplification of the vertebrae, so that in the lower Triassic, various branches of the Labyrinthodonta, independently of each other, become Stereospondyli." He asserts that the Rhachitomi and Stereospondyli should be called older and younger groups of the Labyrinthodonta; logically he would have the same view of the Embolomeri and the stages intermediate between it and the Rhachitomi.

Notable among such transition forms are *Pholidogaster*, *Leptophractus*, and the forms described by Tillotson from West Virginia which are rhachitomoid embolomers, and *Benthosuchus*, *Wetlugasaurus*, and perhaps the many forms mentioned by Huene, which are intermediate between the Rhachitomi and the Stereospondyli, the neorhachitomids. To these must be added the Seymouriamorphs if they are placed among the Stegocephalia.

As in most cases where an attempt has been made to trace the origin of any phylogenetic line, increasing knowledge has resulted in a tendency to place the ancestral form at an ever more remote period. It is generally agreed that the origin of the Tetrapoda was in some Crossopterygian fish not unlike *Osteolepis*, but Watson (1929) going farther back says, "The Amphibians have arisen from an early unknown group of bony fishes from which the Dipnoi and Osteolepids also sprang." He remarks that *Dipterus valenciennesi* of the Middle Old Red Sandstone is the oldest and most primitive of the Dipterids and is so close to the Crossopterygian *Osteolepis* that there was probably a common ancestor which was the real ancestor of the amphibians. He shows that the Osteolepids have:

1. A large circular occipital condyle.

2. The exoccipitals reach to the large supraoccipital which covers all of the hind-brain (as in the Embolomeri).

3. The fore-brain lies in a cavity in the interorbital septum.

4. The otic capsule has a paroccipital process supporting the tabular and may or may not be in contact with the skull roof as in the Amphibia.

5. There are basipterygoid processes on the basisphenoid for articulation with the pterygoids.

6. There is a long unossified tract in the basicranium between the basioccipital and the basisphenoid which is bounded by the proötics.

7. The cheeks are composed of a variable number of bones. In the Osteolepids the squamosal (a cheek bone) is separated from the supratemporal (a roofing

TABLE 1

Williston /16, N. Am. only	Abel /19	Watson /26, /40	Broili (Zittel) /26	Hay /29, N. Am. only	Huene /31	Smith-Woodward /32	Romer /33	Kuhn /33	Save-Söderberg /35
C. AMPHIBIA	C. AMPHIBIA	C. AMPHIBIA	C. AMPHIBIA	C. AMPHIBIA	C. AMPHIBIA	C. AMPHIBIA	C. AMPHIBIA	C. AMPHIBIA	C. EUTETRAPODA
Sb. C. Stegocephalia O. Temnospondyli	Sb. C. Stegocephalia	O. Labyrinthodontia	O. Stegocephalia Sb. O. Temnospondyli = Labyrinthodontia	Sb. C. Phractamphibia	A. Labyrinthodontia	O. Stegocephalia Sb. O. Temnospondyli	O. Labyrinthodontia	Sb. C. Stegocephalia O. Labyrinthodontia = Temnospondyli	Sp. O. Batrachomorpha O. Labyrinthodonta
Sb. O. Embolomeri	O. Embolomeri	Grade Embolomeri Sp. F. Anthracosauroidiae F. Eogyrinidae F. Paleogyrinidae F. Otocratidae	A. Embolomeri	F. Anthracosauridae	O. Embolomeri Sp. F. Anthracosauridae F. Eogyrinidae F. Paleogyrinidae F. Otocratidae	A. Embolomeri F. Anthracosauridae Genus Eogyrinus Genus Paleogyrinus Genus Otocratia	Sb. O. Embolomeri	Sb. O. Embolomeri Sp. F. Anthracosauroidiae F. Eogyrinidae F. Paleogyrinidae F. Otocratidae	F. Anthracosauridae F. ?Macrerpetontidae
F. Cricotidae	F. Cricotidae	F. Cricotidae Sp. F. Loxommoidiae F. Loxommidae		F. Cricotidae	F. Cricotidae Sp. F. Loxommoidiae F. Loxommidae	F. Cricotidae F. Loxommidae F. Pholidogasteridae	F. Cricotidae F. Loxommidae F. Pholidogasteridae	F. Cricotidae Sp. F. Loxommoidiae F. Loxommidae	
Sb. O. Rhachitomi F. Eryopidae	O. Rhachitomi F. Archegosauridae F. Eryopidae	Grade Rhachitomi F. Archegosauridae F. Eryopidae	B. Rhachitomi F. Archegosauridae F. Eryopidae	F. Archegosauridae F. Eryopidae	O. Rhachitomi F. Archegosauridae F. Eryopidae	B. Rhachitomi F. Archegosauridae F. Eryopidae	Sb. O. Rhachitomi F. Archegosauridae F. Eryopidae	Sb. O. Rhachitomi F. Archegosauridae F. Eryopidae	Sb. O. Capitosauridae F. Eryopidae Sb. F. Eryopinae
F. Zatrachydidae	F. Zatrachydae F. Aspidosauridae	F. Actinodontidae F. Rhinesuchidae F. Zatrachidae	F. Rhinesuchidae F. Zatrachididae	F. Zatrachydidae F. Aspidosauridae	F. Actinodontidae F. Rhinesuchidae F. Zatrachydidae	F. Rhinesuchidae F. Zatrachydidae	F. Rhinesuchidae	F. Actinodontidae F. Rhinesuchidae F. Zatrachydidae	Sb. F. Actinodontinae F. Rhinesuchidae F. Zatrachydidae
F. Trimerorhachidae	F. Trimerorhachidae	F. Trimerorhachidae F. Lydekkerinidae	F. Trimerorhachidae F. Lydekkerinidae	F. Trimerorhachidae	F. Trimerorhachidae F. Lydekkerinidae	F. Trimerorhachidae F. Lydekkerinidae	F. Trimerorhachidae	F. Trimerorhachidae F. Lydekkerinidae	
	F. Micropholidae	F. Micropholidae F. Achelomidae	F. Micropholidae	F. Achelomidae	F. Micropholidae F. Achelomidae E. Melosauridae F. Platyopidae	F. Micropholidae	F. Micropholidae	F. Micropholidae F. Achelomidae F. Melosauridae F. Platyopidae	F. Achelomidae F. Melosauridae
		F. Dwinasauridae	F. Cochleosauridae F. Dwinasauridae		F. Dwinasauridae F. Dendrerpetontidae	F. Cochleosauridae F. Dwinasauridae	F. Cochleosauridae F. Dwinasauridae	F. Dwinasauridae	
F. Trematopsidae F. Dissorophidae Sb. F. Dissorophinae Sb. F. Aspidosaurinae	F. Dissorophidae	F. Trematopsidae F. Dissorophidae Sb. F. Dissorophinae Sb. F. Aspidosaurinae	F. Trematopsidae F. Dissorophidae	F. Trematopsidae F. Dissorophidae	F. Dissorophidae Sb. F. Dissorophinae Sb. F. Aspidosaurinae	F. Trematopsidae F. Dissorophidae		F. Trematopsidae F. Dissorophidae Sb. F. Dissorophinae Sb. F. Aspidosaurinae	F. Trematopsidae
	F. Labyrinthodontidae	Grade Stereospondyli F. Trematosauridae F. Capitosauridae F. Metaposauridae F. Mastodonsauridae	C. Stereospondyli F. Trematosauridae F. Capitosauridae F. Metaposauridae F. Mastodonsauridae	Sb. O. Labyrinthodontes F. Metaposauridae F. Mastodonsauridae	O. Stereospondyli F. Trematosauridae F. Capitosauridae F. Metaposauridae F. Mastodonsauridae F. Rhytidostidae F. Brachyopidae	C. Stereospondyli F. Trematosauridae F. Capitosauridae F. Metaposauridae F. Mastodonsauridae F. Rhytidostidae F. Brachyopidae	Sb. O. Stereospondyli F. Trematosauridae F. Capitosauridae F. Metaposauridae F. Mastodonsauridae F. Brachyopidae	Sb. O. Stereospondyli F. Trematosauridae F. Capitosauridae F. Metaposauridae F. Mastodonsauridae F. Rhytidostidae F. Brachyopidae	F. Capitosauridae F. Mastodonsauridae
	F. Plagiosauridae	F. Brachyopidae O. Adelospondyli F. Lysorophidae F. Adelogyrinidae	F. Brachyopidae C. REPTILIA ?? F. Lysorophidae	F. Lysorophidae	F. Lysorophidae	Sb. O. Adelospondyli F. Lysorophidae F. Adelogyrinidae	Sb. O. Lysorophia	O. Adelospondyli F. Lysorophidae	
	O. Pseudocentrophori	Sb. O. Lepospondyli F. Nectridia	Sb. O. Lepospondyli F. Nectridae	O. Stegocephalia Sb. O. Microsauria	B. Pseudocentromorpha α. Pseudocentrophori Sp. F. Nectrididae = Ptyonidae F. Ceraterpetontidae	Sb. O. Lepospondyli	O. Lepospondyli Sb. O. Nectridae	O. Ichthyostegalia O. Pseudocentrophori	O. Ichthyostegalia
	F. Ptyonidae F. Ceraterpetontidae			F. Ptyonidae F. Urocordylidae F. Amphibamidae	F. Urocordylidae	F. Urocordylidae	F. Ceraterpetontidae F. Urocordylidae	F. Urocordylidae F. Amphibamidae	
	F. Ophiderpetontidae F. Phlegethontidae F. Molgophidae	F. Aistopodae	F. Aistopodae	F. Molgophidae F. Tuditanidae F. Sauropleuridae F. Crossotilidae	Sp. F. Aistopodae F. Ophiderpetontidae F. Phlegethontidae F. Molgophidae	Sb. O. Aistopodae F. Tuditanidae	F. Ophiderpetontidae	F. Phlegethontidae F. Molgophidae F. Tuditanidae	
	O. Gastrocentrophori F. Hylonomidae F. Microbrachidae F. Limnerpetontidae		F. Hylonomidae F. Microbrachidae F. Limnerpetontidae	F. Hylonomidae		F. Dolichosomidae F. Hylonomidae	F. Dolichosomidae	F. Dolichosomidae	
F. Diplocaulidae	F. Diplocaulidae	F. Diplocaulidae	F. Diplocaulidae	F. Diplocaulidae	F. Diplocaulidae (Nectridian)	F. Diplocaulidae	F. Diplocaulidae	F. Diplocaulidae	Steen /38 O. Phyllospondyli F. Melanerpetontidae
	O. Phyllospondyli F. Branchiosauridae F. Acanthostomidae	Sb. O. Phyllospondyli F. Branchiosauridae	Sb. O. Phyllospondyli F. Branchiosauridae	Sb. O. Branchiosauria F. Protritonidae	Sp. F. Branchiosauroidea F. Branchiosauridae F. Colostidae F. Stegopidae F. Peliontidae	Sb. O. Phyllospondyli F. Branchiosauridae	Larval forms ?? F. Branchiosauridae F. Colosteidae F. Peliontidae F. Ichthyostegidae	F. Branchiosauridae	Bulman and Whittard /26 O. Phyllospondili F. Branchiosauridae American forms indet. F. Melanerpetontidae F. Eugyrinidae
		F. Melanerpetontidae F. Eugyrinidae F. Miobatrachidae							

bone) by the spiracular cleft. This cleft is represented by the ligamentous attachment of the squamosal to the supratemporal in *Eugyrinus*.

8. The pterygoids are broad, leaving only a small interpterygoid vacuity, and are movably articulated to the basipterygoid processes of the basisphenoid.

From such an inherited structure the amphibians developed along certain well recognized lines, adaptive or nonadaptive. Watson (1926) cites the following:

1. The twelfth nerve, hypoglossal, ceases to penetrate the exoccipital and escapes posterior to the skull.
2. The skull becomes flattened.
3. The brain case becomes less well ossified; the basioccipital, basisphenoid, and supraoccipital become cartilaginous.
4. The occipital condyle originally tripartite, formed of the exoccipitals and the basioccipital, becomes bipartite by the loss of the basioccipital.
5. The cavity for the fore-brain is, in the early amphibians, in the upper part of the thick interorbital septum; later the fore-brain extends downward to lie on the parasphenoid; the tropobasic skull becomes platybasic.
6. The interpterygoid vacuities become steadily larger, as the process of the parasphenoid becomes longer and larger, and the pterygoids cease to be articulated to the basipterygoid processes of the basisphenoid and are sutured to the parasphenoid.
7. The epipterygoid is a small bone resting on the basipterygoid process and on the pterygoid with a *process ascendens* only; in the Permian forms this grows upward into an otic process which acquired attachment to the proötic in the Triassic forms.

The Carboniferous Embolomerids which show the initial stages in the development of these trends have (Watson, 1926):

1. A high skull.
2. A neural cranium exceedingly well ossified; the basioccipital a large bone forming, with or without the participation of the exoccipitals, a single circular occipital condyle; the exoccipitals articulate with the supraoccipital and do not extend anterior to the vagal foramen.
3. The supraoccipital is large extending forward over the proötic.
4. The proötics and opisthotics are fused and have a powerful paroccipital process extending outward and upward to support the tabular; there may or may not be a post-temporal foramen.
5. The anterior part of the fore-brain lies in an excavation of the interorbital septum, whose lower border is clasped by the parasphenoid.
6. The basisphenoid is large and fully ossified with basipterygoid processes for articulation with the epipterygoids and the pterygoids.

TAXONOMY OF THE STEGOCEPHALIA

A large number of generic names have been proposed in the description and discussion of the Stegocephalia but many of these have not been retained in current literature. It will always be impossible to reach an exact agreement in such matters as so much depends on the individual opinion and on the bias of any writer towards the minutiae of distinctions with a multiplication of names, or towards generalization with a reduction in the number of names.

The author has gathered 113 names applied to groups of the Stegocephalia larger than families, 99 of families, and 281 of genera. These include obsolete names, synonyms, varieties of spelling and termination, and certain obvious *lapsi*. No two workers would agree, in all probability, as to which names should be accepted and which rejected but the average would be very nearly the same. The author's carefully considered opinion leads him to reject 108 of the 113 names applied to groups larger than families, 53 of the 99 applied to families, and about 126 of the 281 applied to genera. Practically all of the names are mentioned in catalogues, and in the body of this work, so it is deemed unnecessary to repeat them in a categorical list. The genera figured and described in the following pages are those which, in the opinion of the author, are sufficiently well known to be determinable and usable in discussions of stratigraphy and evolution. Much fragmentary material has received distinctive names but is so debatable as to form and relationship as to be more of an encumbrance than a help in understanding the Stegocephalia. Much of such material had better be dropped from scientific consideration.

STRATIGRAPHY OF THE BEDS CARRYING STEGOCEPHALIA

The natural check upon any phylogenetic arrangement suggested by the morphology of the Stegocephalia would be the establishment of the time relationship of the beds in which the remains occur. It is very uncertain that this necessary check has been applied in some of the published phylogenies. The difficulty in establishing the time relations between fossiliferous beds lies in their wide geographical separation, as those of South Africa and Russia, and in the difficulty of establishing the synchroneity of terrestrial (continental) and marine deposits of the same time interval, on the two sides of a shifting shoreline.

The very general orogeny which occurred at or near the end of the Carboniferous introduced a time of shifting sea borders and of extensive erosion on the land. A large quantity of terrigenous material was swept toward and into the sea and its front alternately and irregularly advanced and retreated with the shifting of the sea border. The relatively enor-

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mous amount of terrigenous material, as compared with the marine, caused a great thickening of the beds toward the land side. With each retreat of the sea a great wedge of terrestrial material was formed which was covered by marine in the next advance of the sea. The marine deposits, continuous at depth, presented a serrate landward edge with wedges of terrestrial between the separated layers. While the increment of the marine remained fairly constant, the total of marine and terrestrial was greatly increased.

Such conditions occur in the Mid-Continent area of North America where the Carboniferous and Permian limestones are intercalated with the terrestrial beds of Oklahoma and Texas. Similarly the limestones of the Russian Basin are intercalated with terrestrial matter and greatly thickened on the foreland of the Urals. Good illustrations of this are given in the cross sections published by Dunbar in the *Bulletin of the American Association of Petroleum Geologists* **24** (2), 1940, and by Kay, *ibid.* **25** (7), 1941.

Where sections can be made in detail the penetration of layers of limestone some distance upon the normally landward side may time the adjacent terrestrial beds, but where such sections cannot be made the correlation is impossible. For this reason many terrestrial beds have been timed by the contained fossil remains, completing a vicious circle; for where the sequence of morphological changes was to be checked by their stratigraphic occurrence they are used to time the beds.

Many attempts based on character of material, stratigraphic position, and fossil content have been made to correlate widely separated beds. Any examination of these will show that only large intervals of time can be correlated in the deposits of the several continents. In such intervals of time there might be considerable evolution in diverse environments producing parallelisms, convergences, etc., which would be taken erroneously for phylogenetic series. The sections in the following table are arranged to bring those best known and most prolific in remains of Stegocephalia into position for easy comparison. The generally accepted correlations are shown by the position of the beds in the table; exceptions and more detailed accounts are given below in Notes on the Stratigraphic Table.

NOTES ON THE STRATIGRAPHIC TABLE

NORTH AMERICA

Huene (1940) made the Phoenexville, Popo Agie, Chinle, and Dockum beds equivalent to the Moltena of South Africa, with some question.

J. E. Adams *et al.* (*Bull. Amer. Assn. Petrol. Geol.* **23**: 1673, 1939) say that the Wolfcamp marine includes the time of the Cisco and Wichita-Albany of the marine and terrestrial of north central Texas. The Leonard marine includes the time of part of the Wichita-Albany, all of the Clear Fork, and part of the Double Mountain.

GERMANY

Huene (1925) makes the Plauenschengrund near Dresden equivalent to the Lebach.

RUSSIA AND SOUTH AFRICA

The vertebrate-bearing beds of South Africa and Russia have been divided into horizons or zones indicated by their fossil content. Such an arrangement has long been in use in South Africa, and in 1937 Efremov attempted a similar zonation for the Russian beds. His arrangement was reviewed by Watson in 1942. Both authors published tables setting forth their views which, though not in exact agreement, correspond in all major particulars. The two tables are reproduced below.

Efremov published two papers in 1937. One in the Abstracts of papers before the XVII International Geological Congress in Moscow, and the other "Upon the development of the Permian Tetrapoda in the U.S.S.R. and the division of the Continental Permian into stratigraphic zones." In this second paper he defines a zone as "not a stratigraphic horizon, but as a comparatively long period of existence of a given fauna

WATSON'S TABLE

		TEXAS	U.S.S.R.	SOUTH AFRICA
Triassic	Keuper			Cave sandstone Red beds Ictidosaurian zone
	Muschelkalk	Dockum		Molteno
	Bunter			Cynognathus B
			Z. VI Capitosaurus	Cynognathus A
				Procolophon
Permian	Zechstein		Z. V Benthosuchus	Lystrosaurus
			Z. IV B Scutosaurus	Cistecephalus B*
			Z. IV A Anthodon	Cistecephalus A
				Endothiodon B
				Endothiodon A
	Kupferschiefer		Z. III "Pelycosaurian"	Tapinocephalus
			Z. II Titanophoneus	
			Z. I Rhopalodon	
	Artinsk	Clear Fork Sphenacodon Wichita Ophiacodon		
Carboniferous	Stephanian	Cisco		

*Possibly a Cistecephalus C.

TABLE 2

North America	France	Germany	South Africa	Russia	Russia (Fredericks)	Czechoslovakia	England-Scotland
Upper Triassic							
Phoenixville	Norian	Upper Keuper	Cave ss., red beds				Rhetic
Chinlee	Carnian	Lettenkohl	Molteno				Keuper (Lossie-
Chugwater							mouth and Spynie)
Dockum			Stormberg				
Middle Triassic	Lodian	Muschelkalk			Kampili Calc =		Muschelkalk
	Virglorian	"Middle" Bunter			Zone VI Russia		
					Wetlugian =		
			Up. Beaufort =		Zone V Russia		
			Zones IV, V, VI S. Af.	Tatarian (pars) =	Tatarian =		Bunter (Cutties
Lower Triassic	Werferian	Bunter		Zone IV Russia	Zone IV Russia		Hillock)
	Thuringian	Zechstein	Lower Beaufort =	Tatarian	Tatarian		Magnesian Is.
			Zones I, II, III, S. Af.	Kasanian	Urjuna = Z. III Rus.		
				Cupriferous ss. and	Kraznavidova = Z. II		
				marine Kasanian	Kama		
					Solemansk		
					Ufa = Zone I Rus.		
		Upper Rothliegende		Kungurian	Kungurian		
	Lodevian	Kreuznach		Ufa or Upper Arta	Cupriferous ss. = Z.I.	Mala-Lota	
		Wadern			Sylwa (Solemansk)	Ruprectice	Lower red beds
		Mid. Rothliegende			Iren	Olevetene	Saxonian
		Tholier, Lebach			Sars		
					Chevnoya-Phyecha		
Word					Artinskian		
	Autunian			Artinskian	Shalya		Autunian
Leonard, marine =		Low. Rothliegende		Lower Arta	Diva	Bytouchov	
Clear Fork, continental		Cuseler	Ecca	Sakmarian, Donetzian	Utka	Kostalov	
		Lower Cuseler	Dwyka		Lower Permian	Boscovice (Moravia)	
Wolf Camp, marine =	Stephanian	Ottweiler		Ouralian		Stephanian	Stephanian
Wichita, continental					Sarga	Kuonova	Radstockian Ser.
					Irgina	Tremosna	Radstock Grp.
					Gschel		Farrington Grp.
							Keele Grp.
							Staffordian Ser.
							Newcastle-under-
							Lyme Grp.
Cisco							Etruria Marl Grp.
Danville							Blackband Grp.
Joggins, Linton, Cannel-	Westphalian			Moscovian	Moscovian		Westphalian
ton, Mazon Creek				Samarian	Samarian	Nyran	(Yorkian)
				Serpuchovian	Nyackiovian	Kladnetz	Lanarkian Ser.
						Kladno	
							Carboniferous ls. Ser.
							Upper ls. Grp.
							Lower Coal Grp.
							Lower ls. Grp.
							Carboniferous ss. Ser.
							Oil Shale Grp.
							Cementstone Grp.
	Dinantian						

TABLE 2—(*Continued*)

Greenland	Spitzbergen	Sweden	Mongolia	China	India	Australia	Madagascar	South America	Mexico
		Rhetic				Hawksbury Series		Sao Benito	
						Wianamata		Piramboia	
						Hawksbury ss.			
						Narabeen		Corumbata	
								Rio do Rasto	
	Middle Triassic		Shao Feng Kow						
	(Posidonomya		and Tung hun						
	beds)		Fan						
								Hiatus = Zones IV,	
						Ipswich beds		V, VI, of S. Africa	
					Scythian stage = Pan-	Burrum beds			
				Schichienfeng Ser.	chet = Maleri = Karachi				
						Bowen River coals		Estrado Nova =	
					Chideru = Damuda Raniganj		Ranohira, ?Triassic	Zones I, II, III of South Africa	
					Ironstone shale			Passo Dois	
					Barakar			Rocinha	
								Lower Estrada Nova	
			Ta Lung Ko						
									Wagonoceras bed =
									Word and Bateo of
									Timor
					Kuhm Mu (in Kashmir)			Ecca	Perrenites bed =
								Iraty (= Up. Dwyka)	Leonard = Butan of
				Shihotze Ser.	Talchir stage	Gympie = Lochinvar	Eliva	Palermo	Timor = ?Artinskian
					Kahabari	Bowen River marine		Bonita	
					Talchir glacial	Bowen River glacial			
				Shensi Ser.	Amb stage = Bijori	Up. Carboniferous =		Itarary = Dwyka	
						? Lochinvar		Orleans cong.	
						Mid. Carboniferous			
						Kutting			
Moscovian ?			Kung Hei Tun			Low. Carboniferous			
						Burrundi			
			Ta Lung Ku						
Dinantian ?									
Upper Upper and									
Lower Upper =									
Old Red of									
Bristol and Che-									
mung-Catskill									
Upper Middle									
with vertebrates									

EFREMOV'S TABLE

GERMANY & ENGLAND	U.S.S.R.	SOUTH AFRICA		NORTH AMERICA
	No tetrapods	Cynognathus VI	Up. B.	
Bunt s.s.	VI Capitosaurus	Procolophon V		No tetrapods
	V Benthosuchus	Lystrosaurus IV	M. B.	
No tetrapods	IV Pareiasaurus	Cistecephalus III		
	III Pelycosaur	Endothiodon II	L. Beaufort	
Zechstein	II Titanophoneus	Tapinocephalus I		Double Mountain
	Rhopalodon			
Rothliegende	No tetrapods	Ecca series. No tetrapods	Ecca	Clear Fork
Gaskohle	Lower part continental beds of cupriferous s.s. Lower part of the Tunguz layer, and the lower Permian section of the Kuznezk Basin.			Wichita
			Dwyka	

frequently embracing an entire complex of different beds."

He makes the following remarks on his different zones.

Zone VI, *Capitosaurus* zone, Eotriassic and characterized by the presence of *Capitosaurus* and *Trematosaurus*. It is equivalent to the *Proptychites* and *Otoceras* zones of the Indian marine Triassic. One locality is given as in the upper limestone of the Great Bogdo Mountains near Bashkuntsak lake in the Lake Volga region. In 1940 he correlated the zone with the Kampili Calc of the Great Bogdo Mountains and the Variegated Clays of the southern part of the Chalo Region (former Government Orenberg).

Zone V, *Benthosuchus* zone, equivalent to the Wetlugian horizon of Frederichs and the *Lystrosaurus* zone of South Africa. Characterized by the presence of the Neorhachitomi, *Benthosuchus* and *Wetlugasaurus*, and containing remains of Dinosaurs and late Cotylosaurs. Numerous localities are given. In 1940 he correlated this zone with the Variegated Beds of the Wetluga Stage.

Zone IV, *Pareiasaurus* zone, equivalent to the *Cistecephalus* zone of South Africa. Characterized by the presence of North Dwina forms, *Scutosaurus*, *Insotrancevia*, *Amalitsakia*, *Anna*, *Swinia*, *Kotlassia*, and the neotenic *Dwinasaurus*. The main locality is the North Dwina River. In 1940 he made this equivalent to the Sandy Limestone of the Tatar Series.

Zone III, Pelycosaur zone, equivalent to the *Endothiodon* zone of South Africa. Characterized by the presence of *Platyops* and small Rhyncocephalians and Pelycosaurs. This occurs in the north as more continental beds, as the Suchona beds of Lutevick and the Mezen beds of Zeke. In the south the beds are chemical sediments of the Volga basin, near Kam, and near Kirov on the Wyatka River. In 1940 he correlated this zone with the Transition Beds of limestone and marl of the uppermost Kasanian, "doubtless in part the Urshan Series."

Zone II, *Titanophoneus* zone, equivalent to the lower part of the *Tapinocephalus* zone of South Africa, and including the upper horizons of the Cupriferous Sandstone. Characterized by the presence of Dinocephalians such as *Enobia*, *Moschops*, and a form near *Jonkeria*, and such Stegocephalia as *Melosaurus*, *Platyops*, and *Chalcosaurus*. In 1940 he correlated this zone with the Belabec, continental, and the Conchiferous, marine, horizon of the Kasanian.

Zone I, *Rhopalodon* zone, equivalent to the lower part of the *Tapinocephalus* zone of South Africa, and the Double Mountain of Texas. Characterized by the presence of *Deuterosaurus*, *Discosaurus*, *Zygosaurus*, *Platyops*, and primitive Pareiasaurs and Dicynodonts. The zone is lower Kasanian, or the lower part may be Kungurian. In 1940 he correlates this zone with the Jugov and a part of the Ufa, continental, and with the *Spirifer* horizon, marine, Kasanian.

Watson (1942) in his review of Efremov's 1940 paper makes the following notes.

Zone VI, *Capitosaurus* zone, is equivalent to the *Cynognathus* zone of South Africa because it contains typical *Capitosaurus* and *Trematosaurus brauni*. It is Lower Triassic.

Zone V, *Benthosuchus* zone, lies between the *Cistecephalus* and *Cynognathus* zone of South Africa and must be "essentially equivalent" to the *Lystrosaurus* zone. Characterized by the presence of Neorhachitomids "which have every appearance" of being ancestral to *Capitosaurus* and *Trematosaurus* or *Trematosuchus*, which latter occur in the "middle" Bunter of Berneberg and the *Cynognathus* zone of South Africa.

Zone IV, *Pareiasaurus* zone, equivalent to the two lower horizons of the *Cistecephalus* zone of South Africa. Characterized by the presence of *Anthodon* and *Scutosaurus*.

Zone III, *Pelycosaur* zone, "tied to" zones I and II by the presence of *Platyops* and *Melosaurus* which occur in zone II.

Zone II, *Titanophoneus* zone. *Rhopalodon* and *Titanophis* are "perhaps considerably" later than the top of the Clear Fork of Texas, and earlier, "but not much," than the *Tapinocephalus* zone of South Africa.

Zone I, *Rhopalodon* zone, "tied to" the Clear Fork of Texas by the presence of *Zygosaurus*, a close ally of *Cacops* and *Dissorophus*.

Huene in 1940 said that Efremov's zones VI and V are equivalent to the Lower Triassic of the Karroo, and to a zone located 200 km. east of Umrutschu in

Sinkiang, and to all of the German Bunter. Zone V is equal to the lower Bunter in time.

CZECHOSLOVAKIA

Westoll (1944) said that the beds at Nyran are separated from the Radnitz beds below by a marked stratigraphic break and are mainly upper Westphalian extending into the Stephanian. According to Nemejc the beds at Nyran are equivalent to the very base of the French Stephanian.

Steen (1938) gives the following table of equivalents:

	Basin	Localities	Remarks
Upper Rothliegende	III. Boskovice Furrow	Málá Lhota	The beds in which the amphibia are found fossil are regarded as upper Rothliegendes in age
	II. Lower Silesian Czechoslovakian Basin	Ruprechtice Olevětin	
Lower Rothliegende	— — — — —	Bytouchov Kostalov	Kuonová has a Carboniferous flora i.e., Upper Stephanian. Bytouchov which succeeds Kostalov, has a more typical Permian flora
Stephanian	I *b*. Klado-Slaný-Rakovnik Basin	Kuonová	
Westphalian	I *a*. Pilzen Basin	Třěmošná Nýřāna	The Nýřāny beds have a typical Upper Westphalian flora. In the locality of Tremosna there are two horizons: (*a*) The lower = Up. Westphalian = Nýřāny (*b*) The upper is on the border between Westphalian and Stephanian

ENGLAND AND SCOTLAND

Huene, in 1925, placed the Cutties Hillock beds, near Elgin in Scotland, as Permian, and the Spynie and Lossiemouth beds as equivalent to the German Lettenkohle, the Molteno of South Africa. In 1940 he placed the Cutties Hillock beds as uppermost Permian or lower Triassic. The Lossiemouth, Spynie, and Cutties Hillock beds are possibly equivalent to the Runu beds in southwest Africa and the Rio do Rasto beds of Rio Grande do Sul, Brazil, in their fauna. The beds at Kenilworth, Warwickshire, England, he considered as equivalent to the German Cuseler.

GREENLAND

Säve-Söderberg (1934) locates the Ichthyostegalia-bearing beds in the uppermost Devonian, what he calls the upper part of the upper Devonian, and places them in his table above the Chemung-Catskill of North America, the Bear Island beds, the Evieux of Belgium, and the Victoria beds of New South Wales, Australia.

MONGOLIA

Yuan (1935) notes that in Sinkiang on the north slope of the Tianshan Mountains and in the south part of Dsungaria are *Lystrosaurus*, *Dicynodon*, *Dimetrodon*, etc., which indicate to him equivalence with Middle Beaufort of South Africa, the Panchet of India, the Narabeen of New South Wales, the Dwina region of Russia, and the, perhaps, Elgin of Scotland.

CHINA

Huene (1940) states that in Shansi, southwest of Pekin, occur Dicynodonts which cannot be in beds higher than the *Cynognathus* zone, Middle Triassic, South Africa.

INDIA

Schuchert (1928) considered the Amb equivalent to the middle of the Damuda Series and so approximately equivalent to the Ecca of South Africa.

Huene (1940) considered the Bijori to be of Upper Permian age because *Gondwanasaurus* has its nearest relative in *Benthosuchus*, which occurs in the upper Permian and the Lower Triassic, but as shown in this paper *Gondwanasaurus* is indeterminate. He placed the Panchet as Lower Triassic or Upper Permian and the Maleri as equivalent to the Keuper-Molteno.

SOUTH AMERICA

Huene, in 1933, published a tentative table showing his ideas of the relation of the beds in Brazil to those of other regions. Though no, or few remains of Stegocephalia have been recovered in South America it is altogether probable that such a fauna will be found. Huene's table is reproduced below.

Brazil	South Africa	Germany	Oceanic
Melaphyr layer	Dolerite		
S. Bento-sandstone	Cave sandstone	Rhaetic	Rhaetic
?	Red beds	Upper Keuper	Noric
Rio de Rastro	Molteno sandstone	Lower Keuper Lettenkohle	Karnic Ladinic
Hiatus	Cynognathus z. Procolophon z. Lystrosaurus z.	Muschelkalk Bunter s.s.	Anisic Scythic
Estrada Nova	Cistecephalus z. Endothiodon z. Tapinocephalus z.	Upper Permian Upper Permian Upper Permian	
Iraty Palermo Bonito	Ecca		
Itararé	Dwyka	Lowest Permian	Uppermost Carboniferous

AUSTRALIA

Huene (1940) placed the Wianamatta Beds of the Hawksbury Series in the Upper Triassic as it contains remains of *Capitosaurus*, *Bothriceps*, and the *Platyops* of Stephen which according to Huene is the larval form of some Brachyiopid Stegocephalian.

PHYLLOSPONDYLI

The term Phyllospondyli suggested by Credner in 1891 has been the most generally accepted designation for a group existing more as a concept than as a natural assemblage justified by the specimens that have been repeatedly studied. Its protean character is evidenced by the multiplicity of names applied to it, the diversity of opinions expressed concerning it, the specimens possibly referable to it, the variety of definitions offered for it, and the fluctuation of its content as genera and families have been included or excluded by successive workers.

The extreme to which the uncertainty has gone is illustrated by the action of Kuhn who makes the family Branchiosauridae a catch-all for many uncertain forms and the action of Romer who rejects the Phyllospondyli *in toto* and, following certain earlier suggestions, regards most of the specimens referred to it as larval forms of genera recognized in the adult stage as belonging to other groups of the Stegocephalia. Both of these suggestions are rather "councils of despair" than solutions of the difficulties and neither suggestion has received great credence. There is good reason to retain the group until further evidence and interpretation shall give more conclusive results.

So long as our determinations and distinctions must be made on a limited number of imperfectly preserved specimens, and so long as species and genera are based upon real or apparent differences in structure that are well within the limits of individual variation or are the possible result of posthumous changes and the accidents of preservation, confusion must persist.

The group Phyllospondyli is based on a conception of the structure of the vertebral column, but a large number of genera and species referred to it have been based on the structure of the skull alone. It is not surprising that of the multiplicity of genera and species referred to the Phyllospondyli many, on the basis of additional information, have been referred to other groups and many proposed names have been shown to be synonyms.

The following names have been suggested for the Phyllospondyli but have not displaced it in general use:

Branchiosauria, Nicholson and Lydekker, 1889.
Branchiosauri, Döderlein, 1890.
Hemispondyli, Jaekel, 1909.
Acanthostomi, Jaekel, 1911.
Branchiosauridae, of the Pseudocentromorpha, Huene, 1931.

The characters accepted for the group by all authors are:

Body Newt- or Salamander-like.

Limbs weak, carpus and tarsus unossified; four fingers on the manus.

Girdles well developed; pubis unossified.

Vertebra formed of a single piece, the basidorsal (neurocentrum), or of three pieces, the basidorsal and the basiventrals (intercentra) co-ossified; the walls thin, enclosing a large unconstricted notochordal space; transverse processes present.

Ribs short and straight with simple expanded head or double-headed.

Skull more or less rounded in form; occipital region and brain case cartilaginous; descending flanges from the dermosupraoccipital and tabular; interpterygoid vacuities large; coronoids and splenial reduced.

Teeth conical with large pulp cavity; no or slight infolding of the dentine; often denticles on the palatal bones.

All authors are agreed, at least tacitly, in the conception of the nature of the vertebrae but there has been an increasing tendency to doubt the presence of basiventral elements as specimen after specimen has failed to show them. This trend of opinion is most interestingly shown in the changing definition of the Phyllospondyli from Lydekker, 1889, to Watson, 1940, in which the departure from the conceived presence of the basiventrals and the acceptance of lack of evidence of their presence is clearly brought out. Their absence may be due to their extreme fragility and consequent failure to leave any record, or to an actual absence of ossified elements in life. If their absence were due to immaturity; i.e., if the Phyllospondyli were larval stages of some other group, it would be expected that a considerable number of specimens would be at a stage where ossification had proceeded so far as to leave some record. This hiatus in the evidence is the strongest argument against the larval theory.

Of the twelve families which have been proposed for the Phyllospondyli, only four are clearly recognizable today,[4] the Branchiosauridae, Eugyrinidae, Melanerpetontidae, Miobatrachidae. The Apateontidae was abandoned by its author, the Protritonidae and Peliontidae are synonyms of Branchiosauridae, the Colosteidae (Sauropleuridae) was composed of genera of such uncertain position as to have no value, the Microbrachidae, Acanthostomidae, and Stegopidae have been shown by associated vertebrae to belong to the Lepospondyli or the Rhachitomi. The four valid families were described by Watson (1940). A similar division into four groups was made by Bullard and Whittard (1926), as follows:

[4] The creation of new genera and families on indeterminate material has been so abundant and the difference in opinion as to the proper reference of specimens so great that the literature is practically hopeless. Reference to comprehensive papers on the Phyllospondyli, such as those by Romer and Steen, will show how only the few well preserved and well differentiated specimens can be worth further consideration. Only such are considered in the following pages.

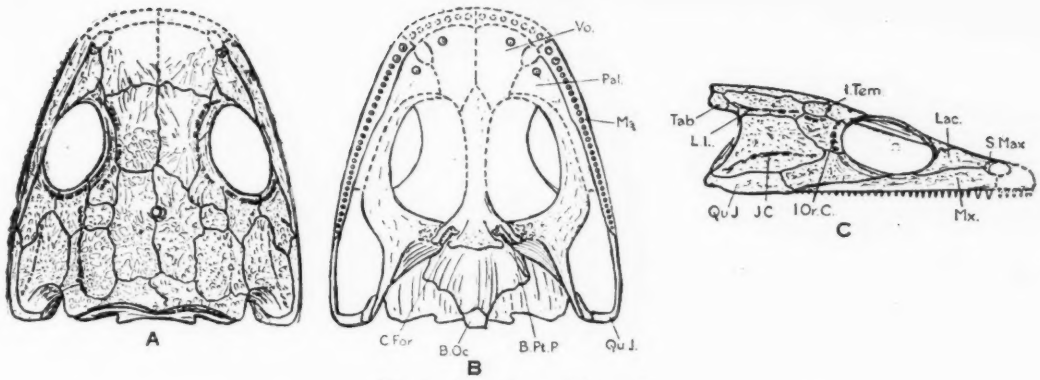

FIG. 1. *Eugyrinus*. Watson.*

1. *Eugyrinus*.
2. *Branchiosaurus*, *Leptorophus*, *Micromelerpeton*, *Pelosaurus*.
3. *Melanerpeton*.
4. North American Upper Carboniferous forms, as *Mazonerpeton*, *Micrerpeton*, *Eumicrerpeton* as yet "practically unknown."

LIST SHOWING THE CLASSIFICATION, GEOLOGICAL HORIZON, AND LOCATION OF THE DETERMINABLE PHYLLOSPONDYLI

Eugyrinidae
- *Eugyrinus*, Lower Coal Measures, of Lancashire, England.
- *Pelion*, Middle Carboniferous, Allegheny Formation, of Linton, Ohio, U. S. A.
- *Branchiosauravus*, Middle Carboniferous, Allegheny Formation, of Linton, Ohio, U.S.A.
- *Saurerpeton*, Middle Carboniferous, Allegheny Formation, of Linton, Ohio, U.S.A.

Branchiosauridae
- *Branchiosaurus*, Lower Permian, Rothliegende, of Germany, France, and Moravia, questionably Middle Carboniferous, Allegheny Formation, of Linton, Ohio, U.S.A.
- *Micromelerpeton*, Lower Permian, of Odersheim, Germany.
- *Leptorophus*, Middle Rothliegende, of the Plauenschengrunde, near Dresden, Germany.
- *Pelosaurus*, *idem* as *Leptorophus*.
- *Macrerpeton*, Middle Carboniferous, Allegheny Formation, of Mazon Creek, Illinois, U.S.A.

Melanerpetontidae
- *Melanerpeton*, Lower Permian, Rothliegende, Moravia.

Miobatrachidae
- *Miobatrachus*, Middle Carboniferous, Allegheny Formation, of Mazon Creek, Illinois, U.S.A.

* The author's name indicates the source of the figure. A,B,C, indicate upper, lower and lateral views of the skull. Owing to the demands of reproduction the photographed figures have been slightly retouched. All figures were intended to be of approximately the same size. The necessities of make-up have caused certain ones to be reduced. This is of no significance.

EUGYRINIDAE

The family was described by Watson (1940) as follows:

> Phyllospondyli, with a skull retaining an intertemporal bone, with a single, largely basioccipital condyle, basipterygoid process near the middle line, interpterygoid vacuities of moderate size.

Eugyrinus (fig. 1 *A*, *B*, *C*) was originally described by Smith-Woodward (1891) as belonging to the genus *Hylonomus*, but was raised to generic rank by Watson (1921) and placed in the family Branchiosauridae. In 1940 he placed it in a new family. The family and generic characters as given by Watson, Steen and others, are:[5]

1. Body comparatively robust, "somewhat later ally compressed" (Smith-Woodward 1891).
2. Tail unknown, probably short.
3. Limbs. Femur moderately long, slender.
4. Girdles like those of *Branchiosaurus;* ilium vertically elongate (Smith-Woodward 1891).
5. Vertebrae like those of *Branchiosaurus*.
6. Ribs short, straight, expanded at both ends.
7. Sculpture of knobs and lines.
8. Scutes of both dorsum and venter, recalling those of *Branchiosaurus;* ventral scutes larger than dorsal (Smith-Woodward 1891).
9. Skull bluntly triangular; occipital condyle single, tripartite, formed by basioccipital and exoccipitals; posterior portion of parasphenoid broad, rhomboidal; interpterygoid vacuities large (or moderate); ectopterygoid present.
10. Orbits oval, in anterior half of the skull; on sides of the skull.

[5] In attempting to collate the descriptions of various specimens it was necessary to consider the same characters in each case. A list of 16 points, the ones most frequently used, was prepared and the characters as given or shown in illustrations were recorded. The absence of any character from the list means that it has not been described or figured. The order of the points has been strictly adhered to throughout the paper in order to facilitate comparison.

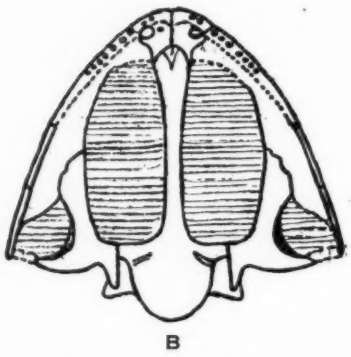

FIG. 2. *Pelion*. Steen.

11. Teeth. Maxillary teeth simple cones; a large tooth on prevomer and palatine; denticles on median portion of prevomer.
12. Nares. External nares small, widely separated, nearly terminal.
13. Lachrymal extending from orbit to naris.
14. Cornua ? small or absent.
15. Inter-temporal present.
16. Otic notch shallow.

Watson (1940) notes that *Eugyrinus* differs from *Branchiosaurus* in the longer, narrower skull, much smaller orbits, smaller posterior portion of the parasphenoid and the presence of an inter-temporal. In 1921 he maintained that *Eugyrinus* showed a precocious specialization in the direction of chondrification although from the Lower Coal Measures—"it agrees in stage (of chondrification) with Upper Permian Labyrinthodonts. *Branchiosaurus* with one from the Upper Triassic." This is particularly evident in the shape of the parasphenoid and the size of the interpterygoid vacuities. It is (Watson 1940) advanced beyond the typical Embolomeres in the greater flattening of the skull, the reduced cartilage bones, the development of cartilaginous flanges on the dermosupraoccipital and the enlarged interpterygoid vacuities. He considered *Eugyrinus* as the sole member of the family but called attention to its close resemblance in many ways to the Lepospondyl *Amphibamus*.

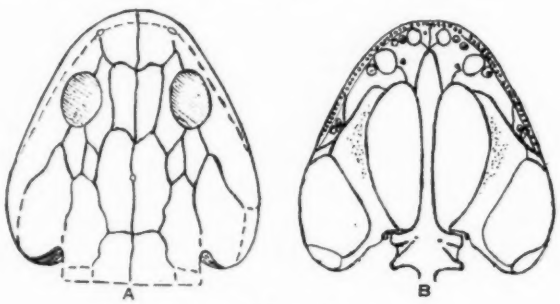

FIG. 3. *Pelion*. Romer.

Pelion (fig. 2 *B*, 3 *A*, *B*) was placed in the Branchiosauridae (Smith-Woodward, Kuhn), Peliontidae (Moodie, Abel, Romer) and the Phyllospondyli *incert. sed.* (Steen). Certain specimens previously referred to other genera were regarded by Romer (1930) as belonging in the genus *Pelion* and finally (1938) he suggested that *Pelion* "may be a larval form of *Leptophractus*." It is evident from Romer's (1930) description of the skull of *Pelion* that it must be near *Eugyrinus*, if not in the same family. The disproportion in size of the limbs of *Pelion* is not usable as a distinction as the limbs are unknown in *Eugyrinus*.

Romer's description of the family Peliontidae (1930), which includes that of the genus, is

> primitive branchiosaurs differing from the more typical forms in the presence of an intertemporal. The palate is primitive including such features as a movable articulation of the pterygoid with the basipterygoid process, the retention of the ectopterygoid, etc.

The characters are:

2. Tail relatively short.
3. Limbs. Posterior limbs elongate; carpus and tarsus cartilaginous.
8. Scutes "cycloidal."
9. Skull height one-third of the breadth; a peculiar posterior extension of the parasphenoid; pterygoid movably articulated to the parasphenoid (or touching it); interpterygoid vacuities large; ectopterygoid present; anterior palatal vacuities present, small.
10. Orbits far forward, oval, separated.
11. Teeth. Denticles on the pterygoid, large teeth on prevomers, palatines and ectopterygoids.
12. Nares. External nares small, nearly terminal.
13. Lachrymal extending from orbit to naris.
14. Cornua ? absent (skull injured posteriorly).
15. Intertemporal present.
16. Otic notch shallow.

Romer (1930) says the "palate of *Pelion* tends strongly to confirm Watson's thesis that the branchiosaurs are descended from primitive labyrinthodonts, or at least from forms with a skull structure of a type found in primitive members of that group." And "The postcranial skeleton, so far as preserved, is in agreement with this conclusion" (that *Pelion* is a primitive branchiosaur).

Branchiosauravus (fig. 4 *A*, 5 *A*), for "*Erpetosaurus*" *tabulatus*, is also referred to by Romer (1938) as the possible larval form of *Leptophractus lancifer*. His interpretation of the specimen does not agree with that of Moodie. The genus was placed in the Peliontidae by Romer (1930) because of primitive characters, which would place it preferably in the family Eugyrinidae. The list of generic characters is but a repetition of those of that family.

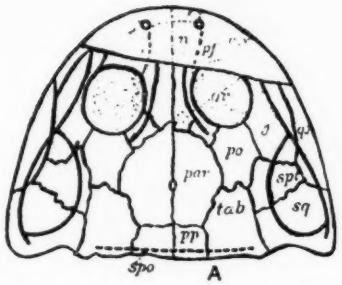

FIG. 4. *Branchiosauravus*. Moodie.

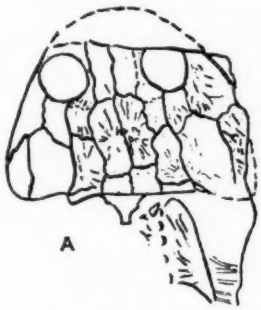

FIG. 5. *Branchiosauravus*. Romer.

5. Vertebrae, 25 presacrals.
6. Ribs short and nearly straight, larger than in typical Branchiosaurs.
7. Sculpture a pitted center with radiating and branching ridges.
8. Skull short and broad; outline of the roof bones "very similar" to that of *Eugyrinus;* ectopterygoid present.
10. Orbits large, round, nearly lateral; in anterior half of the skull.
14. Cornua absent or very small.
15. Intertemporal absent but suggestion from sculpture that it is present but coössified with the postfrontal.
16. Otic notch shallow.

Saurerpeton (fig. 6 *A*), based on *Sauropleura latithorax*, has been placed in the Sauropleuridae (Moodie) Urocordylidae (Kuhn), and Peliontidae (Romer). The latter regarded it as a synonym of *Pelion*. The characters are nearly the same as those of the Eugyrinidae, differing only in the teeth and the intertemporal. In the lack of knowledge of the vertebrae its position is uncertain. Perhaps the lack of an intertemporal may place it in the Branchiosauridae if it is a Phyllospondyl.

1. Body short and broad.
3. Limbs. Anterior pair short and heavy.
4. Girdles. Thoracic well developed, interclavicle oval.
6. Ribs long, slender, "non-alate" (or short, slightly curved, Moodie).
7. Sculpture of pits.
8. Scutes on venter, broad, imbricate, in chevron pattern.
9. Skull broad, rounded.
10. Orbits large, oval; in anterior half of the skull, widely separated.
11. Teeth heterodont.
12. Nares. External nares small, nearly terminal.
13. Lachrymal absent (or fused with prefrontal).

BRANCHIOSAURIDAE

Watson's description (1940) is:

Phyllospondyli, with a flattened skull from which the intertemporal has been lost with paired ex-occipital condyles, basipterygoid processes widely separated, interpterygoid vacuities large, the ectopterygoid lost, and the enlarged subtemporal fossa stretching forward to a point immediately behind the palatal nostril.

The characters are:

1. Body salamander-like, 2½ times as long as the tail.
2. Tail relatively short, vertically expanded.
3. Limbs weak, carpus and tarsus cartilaginous.
4. Girdles well developed; pubis cartilaginous.
5. Vertebrae ? without ventral elements.
6. Ribs short, straight, single headed.
8. Scutes present on venter at least.
9. Skull approximately as long as broad; occipital condyle double; basipterygoid process moveably articulated to the pterygoid; interpterygoid vacuities large; ectopterygoid absent.
10. Orbits large, oval, in anterior half of the skull.
11. Teeth on jaws with large pulp cavity; dentine simply infolded; denticles on all palatal bones.
12. Nares. External nares small, terminal; internal nares lateral.
13. Lachrymal extending from orbit to naris.
14. Cornua represented on the tabular by a facet for a posttemporal or for muscular attachment.

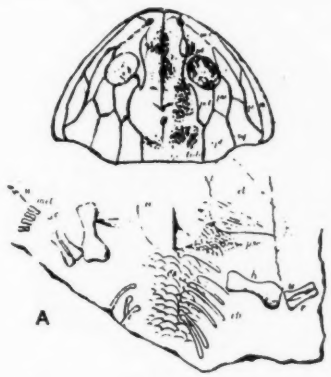

FIG. 6. *Saurerpeton*. Moodie.

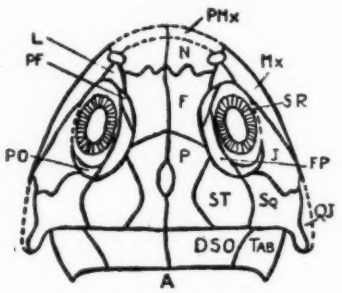

FIG. 7. *Branchiosaurus*. Whittard.

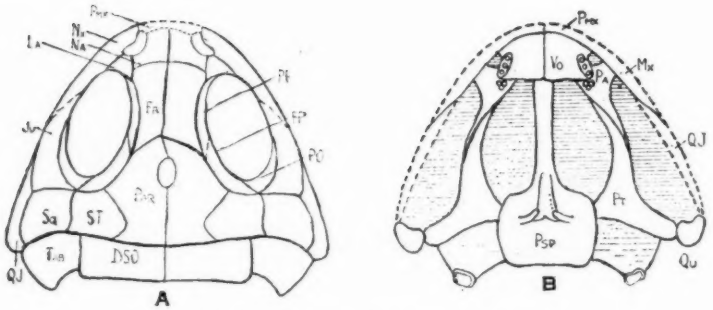

FIG. 8. *Branchiosaurus*. Bulman and Whittard.

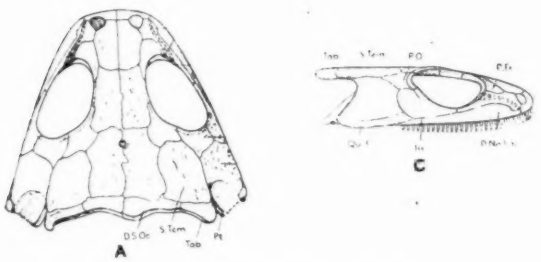

FIG. 9. *Branchiosaurus*. Watson.

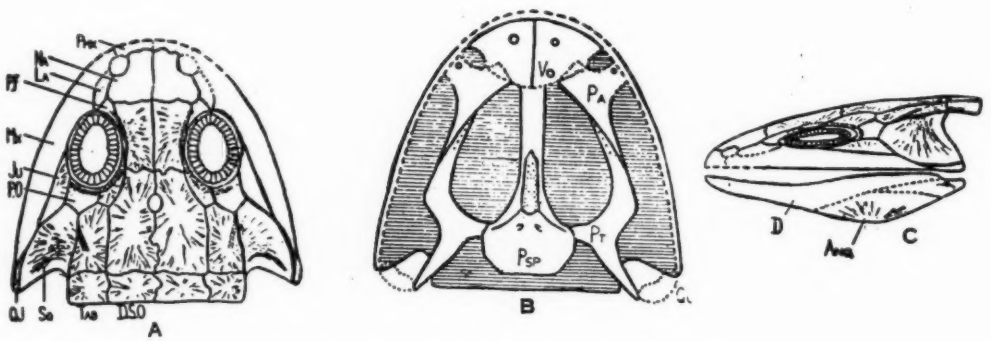

FIG. 10. *Micromelerpeton*. Bulman and Whittard.

15. Intertemporal absent.
16. Otic notch present, not deep.

Repeated study of specimens has cast doubt on the presence of ventral elements in the vertebrae. The absence of such elements in the fossils has been explained in various ways, as noted above. Romer's argument (1939) that the elements were present in the cartilaginous condition because of immaturity is reasonable but the language in which it is presented emphasizes its speculative character and the lack of positive evidence. He says (1939)[6] that all the vertebrates above the Cyclostomes have central (ventral elements) cartilages and that "there is *no reason to believe*" that they were absent in the Phyllospondyli. "Upon *our inferences* as to the nature of these cartilages rests the determination of the proper phylogenetic position of the branchiosaurs." "Of what nature were the *cartilaginous centra present* in branchiosaurs?"—but the cartilaginous centra were only *inferred* to be present. "We may reasonably *infer* that the *unknown* central cartilages were intercentra and pleurocentra of the Labyrinthodont type." The reasoning is plausible but in itself emphasizes the lack of evidence. If the branchiosaurs are the result of a precocious chondrification of an embolomerous stage the excessive progress in the ventral elements is a characteristic of ordinal value, but here the evidence is only cumulative, not conclusive.

It is to be noted that even in the smallest specimens of *Branchiosaurus* known, still retaining the evidence of gill structures (Credner, Die Stegocephalen und Saurier des Plauen'schen Grunde, pl. XVII, fig. 31, 1886), the character of precocious enlargement of the interpterygoid vacuities is well developed, fully as much proportionately as in the largest (oldest) specimens. This argues strongly against the larger forms being larvae of other stegocephalians.

Branchiosaurus (fig. 7 *A*, 8 *A*, *B*, 9 *A*, *C*) has several synonyms, *Pleuroneura*, *Protriton*, and possibly (Romer 1930) certain species of *Tuditanus* and *Erpetosaurus*. The characters are those of the family.

[6] The italics are by the present author.

Micromelerpeton (fig. 10 *A*, *B*, *C*) is placed in the Branchiosauridae (Bulman and Whittard, Smith-Woodward, Kuhn). Its characters are:

1. Body narrow, elongate.
3. Limbs short, powerful; carpus and tarsus cartilaginous.
4. Girdles robust; pubis unossified.
5. Vertebrae. 20–30 presacrals.
6. Ribs short, straight.
7. Scutes comparatively large.
9. Skull triangular, obtuse, nose wide as long, occipital region rectangular; tabulars almost square; maxillary forms practically the whole lateral margin; jugal and quadratojugal small; sensory canals present; ectopterygoid absent.
10. Orbits small, elliptical, in anterior half of the skull.
11. Teeth. Denticles on parasphenoid process and anterior end of the palatine; large teeth on prevomer and palatine.
12. Nares. External nares small and nearly terminal. Internal nares good sized, lateral.
13. Lachrymal extending from orbit to naris.
14. Cornua absent.
15. Intertemporal absent.
16. Otic notch wide.

Leptorophus (fig. 11 *A*, *B*), founded on *Branchiosaurus tener*, is placed in the Branchiosauridae (Bulman and Whittard, Smith-Woodward, Kuhn). Its characters are:

1. Body of considerable size.
3. Limbs. Humerus and femur long and narrow; phalangeal formula 2, 2, 3, ?–2, 2, 3, 4, 3.
4. Girdles. Thoracic like that of *Branchiosaurus*, the bones extremely light and fragile; pubis unossified.
5. Vertebrae ? 21–23 presacrals, 1 sacral, 14 caudals.
7. Sculpture fine pits and striae.
9. Skull elongate oval; bones of roof very thin; palatines Y-shaped; parietals elongate; quad-

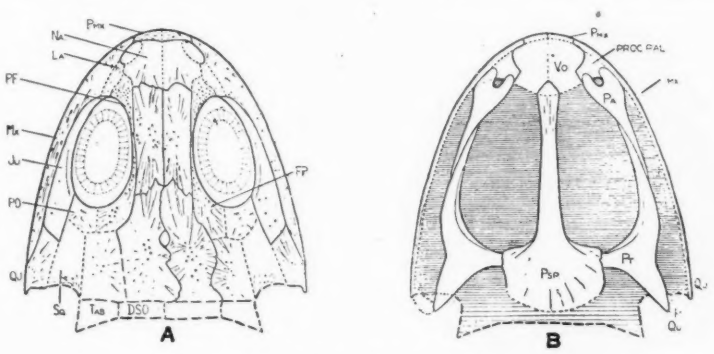

FIG. 11. *Leptorophus*. Bulman and Whittard.

ratojugal large, rectangular; jugal and maxillary large; squamosal "remarkably thin and fragile, in contrast to the large massive type found in *Pelosaurus* and *Micromelerpeton*." (Bulman and Whittard 1926.)
10. Orbits large, oval, in anterior half of the skull.
11. Teeth. Denticles on posterior part of the parasphenoid process.
12. Nares. External nares oblique, nearly terminal.
13. Lachrymal practically excluded from the orbital margin.
14. Cornua ? absent.
15. Intertemporal absent.
16. Otic notch shallow.

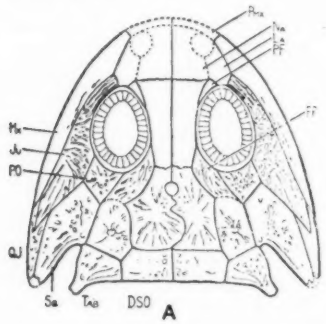

FIG. 12. *Pelosaurus*. Bulman and Whittard.

Pelosaurus (fig. 12*A*) is placed in the Branchiosauridae by all who mention it. The characters are:

1. Body lizard-like.
3. Limbs short and robust.
4. Girdles. Pubis unossified.
6. Ribs short, almost straight.
7. Sculpture radial.
8. Scutes small, rhomboidal, on venter.
9. Skull triangular, rounded anteriorly to an elliptical curve; brain case projecting somewhat backward; jugals large; parasphenoid large with long, slender process; sensory canals absent.
10. Orbits large, in anterior half of the skull.
11. Teeth pointed, curved; dentine infolded.
14. Cornua stout and slightly curved.
15. Intertemporal absent.
16. Otic notch narrow, large.

Macrerpeton caudatum is put in the Branchiosauridae (Smith-Woodward, Kuhn, Moodie). The specimen is an impression in a nodule, remarkable in that it shows something of the lateral line upon the body and something of the color markings of the body. Few of the osteological features of the skull are apparent. It is probably a Phyllospondyl but otherwise indeterminate.[7] The characters are:

1. Body small, salamander-like.
2. Tail elongate, laterally compressed.
3. Limbs stumpy and heavy; femur relatively longer and more slender than the humerus.
5. Vertebrae. 20–21 presacrals.
6. Ribs short, straight, heavy, single headed.
8. Scutes in chevron pattern on venter. Caudal scutes ovoid or rounded with radiating lines (Moodie).
9. Skull short and broad, resembling *Branchiosaurus*.
10. Orbits large, broadly oval, anterior.
12. Nares. External nares small, terminal.
15. Intertemporal ? absent. An anterior projection of the supratemporal between the postfrontal and postorbital may represent this bone.

Many of the forms placed in the Branchiosauridae must be regarded with reserved judgment. Most have been referred to the family on skull characters which have been repeatedly shown in other forms to vary with age, or have been differently interpreted from imperfect material. Several have been shown to possess Labyrinthodont vertebrae and several names have been shown to be synonyms. Moreover, if the present tendency to regard the Branchiosaurs as precociously chondrified should prove to be on the right line, the possibilities of recognizing parallelisms in adaptation are so great as to render geologic age one of the determining criteria. This is almost useless with the Branchiosaurs as they extend from the Lower Carboniferous to the Permian. Leaving to one side Kuhn's inconclusive use of the Branchiosauridae and Romer's entire rejection of the Phyllospondyli, the following forms have been regarded as indeterminate but nearest to the Branchiosauridae; at least as Phyllospondyli.

Apateon
Dawsonia
Eumicrerpeton
Mazonerpeton
Mytaras (fig. 13*B*)
Tungusogyrinus

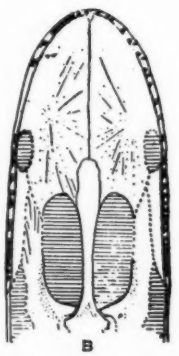

FIG. 13. *Mytaras*. Steen.

[7] *Macrerpeton huxleyi* is referred to the Embolomeri by Romer (1930).

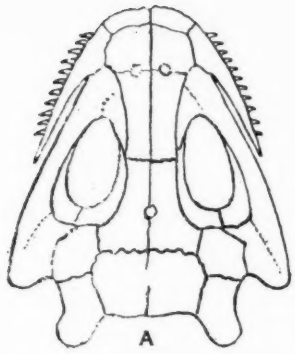

FIG. 14. *Melanerpeton*. Augusta.

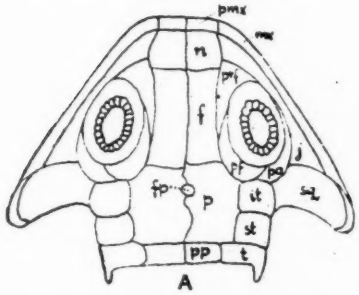

FIG. 15. *Melanerpeton*. Augusta.

MELANERPETONTIDAE

Watson (1940) gives the following description of the family:

Incompletely known advanced Phyllospondyli in which an intertemporal bone is retained, and the interclavicle has a long posterior process.

This, with Steen's (1938) description can be summarized as follows:

4. Girdles. Thoracic girdle, interclavicle with long process; clavicle bent.
9. Skull. Occipital region extends far behind articulation for the lower jaw. Augusta (1936) speaks of the "surprising" posterior extension.
10. Orbits large, oval, in midlength of skull.
12. Nares. External nares anterior and lateral.
13. Lachrymal absent.
14. Cornua small, but prominent.
15. Intertemporal present.
16. Otic notch broad and deep.

Melanerpeton (fig. 14*A*, 15*A*) was but in the Branchiosauridae (Smith-Woodward, Kuhn, Abel) and in the Melanerpetontidae (Watson, Steen). The characters are those of the family.

MIOBATRACHIDAE

Watson's description is as follows (1940):

Phyllospondyli in which the flattened skull has lost both intertemporal and supratemporal, the bones of the tabular row have either disappeared or are fused into a smooth sloping occiput so that the skull roof ends at the hinder border of the parietals. The occipital condyle seems to be single, the basipterygoid processes are widely separated, and the hinder part of the parasphenoid is very wide. The interpterygoid vacuities are very large, but the ectopterygoid is retained and the subtemporal fossa is small. There are small subnotochordal "central" bones.

The characters are:

5. Vertebrae appear to be rhachitomous but may be modified embolomerous.
6. Ribs 10, slender, gently curved, two-headed.
8. Scutes. Minute polygonal plates under orbit; a scaly plastron.
9. Skull. Parietals form whole of the posterior border of the ornamented table; no tabulars or postparietals (dermosupraoccipitals) visible; no supratemporals; sensory grooves absent; ecto-

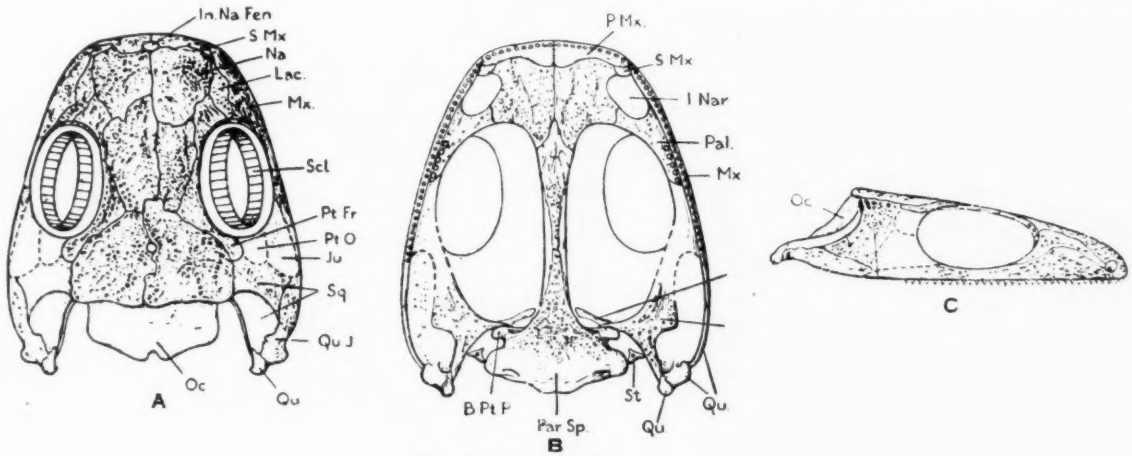

FIG. 16. *Miobatrachus*. Watson.

pterygoid ? absent; interpterygoid vacuities large ("extreme"); parasphenoid very large posteriorly; lower surface of the septomaxillary appears on the palatal surface; stapes short, triangular, perforate; epipterygoid present; an interpremaxillary vacuity.
10. Orbits large, 22 plates in the sclerotic ring.
11. Teeth. Denticles on all palatal bones.
12. Nares. External nares small, widely separated, nearly terminal.
13. Lachrymal extends from orbit to naris.
14. Cornua ?
15. Intertemporal absent.
16. Otic notch shallow.

Miobatrachus (fig. 16*A*, *B*, *C*) is the sole genus and has the characters of the family.

LEPOSPONDYLI

The group Lepospondyli, also called Microsauria, Holospondyli, and Gastrocentrophori, has been characterized as having the vertebrae formed by the basidorsal and basiventral elements which are coossified so closely that there is no trace of a suture between the neural arch and the centrum. The notochordal canal is continuous through the centrum but contracted within it, justifying the common description, "centrum hourglass-shaped in longitudinal section." The ribs are elongate, curved, and frequently bicipital. The teeth are conical, hollow, and with little or no infolding of the dentine. The limbs are of various proportions from practically absent to well developed and lizard-like. The skull is of various size and form. The result of such a loose definition is that, except where the vertebrae are preserved, reference to the group is uncertain. Many forms known only from the skull, or from inadequate, fragmentary material, have been assigned to the group without sufficient evidence. Dawson, who used the name Microsauria, and the late George Baur saw in this group the ancestral forms from which the reptiles arose, a position that is no longer tenable. The group, as conceived, has been laden with so many heterogeneous and poorly understood forms that it is very proper to question its coherence. Watson (1940) says of the Microsauria, "if, indeed, it has any real existence." And, the Lepospondyli "contain a great and obviously heterogeneous mass of animals." His definition of the Lepospondyli in 1929 was, "Stegocephalian Amphibia in which the vertebrae are composed of a continuous mass of bone, of unknown homologies, in which no suture can be seen."

There have been proposed 20 families of the group, a number which in itself indicates the uncertainty of the taxonomic boundaries.

Amphibamidae, Moodie, 1910.
Ceraterpetontidae, Broili, 1905.
Colosteidae, Cope, 1875.
Crossotelidae, Williston, 1909.
Dendrerpetontidae, Fritsch, 1885.
Diplocaulidae, Cope, 1880.
Dolichosomatidae, Lydekker, 1889.
Hylonomidae, Fritsch, 1883.
Hyloplesiontidae, Lydekker, 1889.
Ichthycanthidae, Moodie, 1916.
Limnerpetidae, Lydekker, 1889. (Limnerpetontidae, Abel, 1919)
Microbrachidae, Lydekker, 1889.
Molgophidae, Cope, 1878.
Nyranidae, Lydekker, 1889.
Ophiderpetontidae, Romer, 1930.
Phlegethontidae, Cope, 1875.
Ptyonidae, Cope, 1875.
Sauropleuridae, Hay, 1902.
Tuditanidae, Cope, 1875.
Urocordylidae, Lydekker, 1889.

Of this number the Amphibamidae, Ceraterpetontidae, Diplocaulidae, Dolichosomatidae, Microbrachidae (Hylonomidae), Urocordylidae, ?Ophiderpetontidae, and ?Sauropleuridae are recognized today. The Molgophidae and Phlegethontidae are synonymous with the Dolichosomatidae. The Hyloplesiontidae and Hylonomidae are synonymous with the Microbrachidae. Westoll (1943), following suggestions by Steen and Watson, would place the Microbrachidae (Hylonomidae) in the Adelospondyli. The Colosteidae was regarded by Hay as a synonym of the Sauropleuridae; Romer suggested that it might belong in the Phyllospondyli but later abandoned that group. The Ptyonidae, Tuditanidae, and Limnerpetontidae have been shown to be made up of forms with diverse characters. The Crossotelidae, known only from the vertebrae, may belong in the Diplocaulidae or the Urocordylidae. The Nyranidae, Ichthycanthidae, and Dendrerpetontidae have been shown to belong in the Rhachitomi.

List Showing the Classification, Geological Horizon, and Location of the Determinable Lepospondyli

Amphibamidae
- *Amphibamus*, Middle Carboniferous, Allegheny Formation of Mazon Creek, Illinois, U.S.A.
- *Cephalerpeton*, Middle Carboniferous, Allegheny Formation, Mazon Creek, Illinois, U.S.A.

Ceraterpetontidae
- *Ceraterpeton*, Coal Measures of Kilkenny, Ireland. Coal Measures of Staffordshire, England.
- *Diceratosaurus*, Middle Carboniferous, Allegheny Formation, of Linton, Ohio, U.S.A.
- *Eoserpeton*, *idem* as *Diceratosaurus*.

Dolichosomatidae
- *Dolichosoma*, Coal Measures of Kilkenny, Ireland. Upper Westphalian of Nyran, Czechoslovakia.
- *Ophiderpeton*, *idem* as *Dolichosoma*.

XUM

Phlegethontia, Middle Carboniferous, Allegheny Formation, of Linton, Ohio, U.S.A.
Molgophis, *idem* as *Phlegethontia*.
Ichthyerpeton, Coal Measures of Kilkenny, Ireland. Middle Carboniferous, Allegheny Formation of Linton, Ohio, U.S.A. (? an Embolomerid).

Diplocaulidae
Diplocaulus, Lower Permian, Wichita and Clear Fork, of Texas, U.S.A. Middle Carboniferous of Vermillion County, Illinois, U.S.A.
Permoplatyops, Lower Permian, Clear Fork, of Texas, U.S.A.
Batrachiderpeton, Coal Measures near Edinburgh, Scotland.

Microbrachidae (Hylonomidae)
Hylonomus, Carboniferous of South Joggins, Nova Scotia. Questionably, Rothleigende, from the Plauenschengrund, near Dresden. Questionably, Westphalian and Stephanian, of Nyran and Kuonova, Czechoslovakia.
Hyloplesion, Westphalian of Nyran and Tremosna, Czechoslovakia.
Microbrachis, Westphalian, of Nyran, Czechoslovakia.

Urocordylidae
Urocordylus, Coal Measures, of Kilkenny, Ireland. Questionably, Middle Carboniferous, Allegheny Formation, of Linton, Ohio, U.S.A. Questionably, Westphalian, of Nyran, Czechoslovakia.
Ctenerpeton, Middle Carboniferous, Allegheny Formation, of Linton, Ohio, U.S.A.
Lepterpeton, Coal Measures, of Kilkenny, Ireland.
Scincosaurus, Westphalian, of Nyran, Czechoslovakia.

Colosteidae
Colosteus, Middle Carboniferous, Allegheny Formation, of Linton, Ohio, U.S.A.

AMPHIBAMIDAE

The Amphibamidae occupy a most uncertain position; the family is generally placed in the Lepospondyli but, as shown below, Romer and Watson have placed it in the Phyllospondyli near *Branchiosaurus*. The characters of the family Amphibamidae are:

1. Body short and broad, less than 3 inches total length.
2. Tail short and stumpy.
3. Limbs short and stout; digits clawed.
4. Girdles well developed; pubis of calcified cartilage.
5. Vertebrae with short centra; about 25 presacrals.
6. Ribs long, curved (Moodie); short (Watson).
7. Sculpture a faint ornament of shallow pits.
8. Scutes hexagonal, relatively thick.
9. Skull large ("huge"); dorsal surface flat, snout rounded, cheeks cylindroidal passing gradually from horizontal upper to vertical lateral faces; tabulars, dermosupraoccipitals, and supratemporals absent; a broad sheet of smooth bone with a median ridge lies posterior to the parietals, sloping rapidly downward; epipterygoid present; interpterygoid vacuities large.
10. Orbits large, oval, widely separated; in anterior half of the skull.
11. Teeth small, anisodont, conical, sharp; dentine not infolded.
12. Nares. External nares relatively small, transversely oval.
13. Lachrymal reaching from orbit to naris.
14. Cornua absent.
15. Intertemporal absent.
16. Otic notch deep and extensive.

Amphibamus (fig. 17*A*, *B*, *C*) was described by Moodie (1916) as a Microsaur and he gave a full description of the vertebrae which are of a distinctly Lepospondylous type. Disregarding the character of the vertebrae Romer (1930) says *Amphibamus* is a "rather primitive Branchiosaur," with no further comment. Watson (1940) regarded it as a Phyllospondyl, or as closely related to that group. He said, "*Miobatrachus* and *Amphibamus* have no relationship

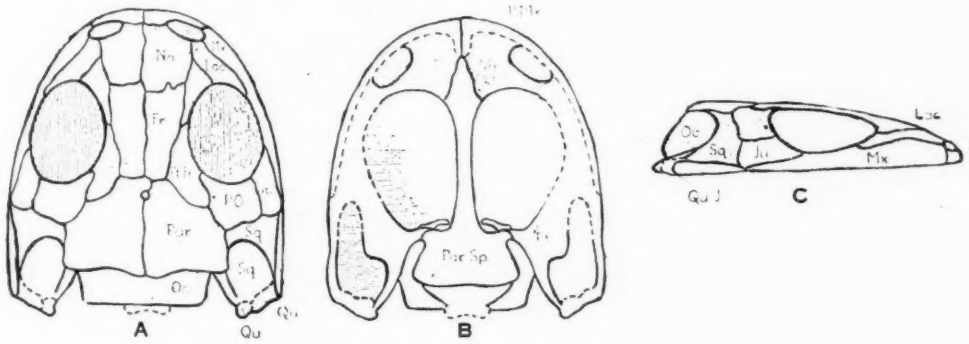

FIG. 17. *Amphibamus*. Watson.

to the adelospondylus Microsaurians," and "*Amphibamus* is intermediate between *Miobatrachus* and *Eugyrinus*." The assertions of Romer and Watson are based upon the structure of the skull, neglecting Moodie's description of the vertebrae which Watson admits "appears to be essentially correct." To increase the confusion Watson refers to "adelospondylous Microsaurians." Moodie and most other writers use the terms Microsauria and Lepospondyli as synonymous; to reject the evidence of the vertebrae is to reject the most stable element in the classification of the Stegocephalia.

The characters are those of the family.

Cephalerpeton is placed in the Amphibamidae by all who mention it. It was distinguished from *Amphibamus* by Moodie by its larger size, anisodont teeth (an error), and lack of an otic notch. No restoration has been published. Its characters are:

1. Body larger than that of *Amphibamus*, reaching 6 inches total length.
10. Orbits nearer midlength of skull.
11. Teeth isodont.
16. Otic notch absent or slight.

Erpetocephalus is so imperfectly known that most authors have regarded it as indeterminate. Kuhn placed it in the Amphibamidae. The name has been regarded as a synonym of *Ichthyerpeton* (Lydekker), and *Ichthycanthus* has been regarded as a synonym of it (Kuhn).

Such characters as can be made out from Huxley's figure are:

9. Skull broad and blunt.
10. Orbits large, separated, in anterior half of the skull.
15. Cornua absent but tabular a little extended.
16. Otic notch deep and narrow.

CERATERPETONTIDAE

Romer (1930) placed in this family most of the genera placed by others in the family Urocordylidae. The first use of the family name (so far as the author has been able to determine) was by Jaekel in 1903, but neither he nor Broili (1905) defined it. *Ceraterpeton*, *Diceratosaurus*, and *Eoserpeton* are grouped together by most writers but with different suggested relationships and associates. Hay put them in the Urocordylidae; Abel in that family with *Scincosaurus*, *Diplocaulus*, and *Batrachiderpeton;* Romer considered *Ceraterpeton* and *Eoserpeton* as synonyms of *Diceratosaurus;* Steen considered *Scincosaurus* as a synonym of *Ceraterpeton*.

The families Ceraterpetontidae and Urocordylidae have been used almost interchangeably but direct comparison shows a few but significant differences, notably in the limbs, cornua, and otic notch.

The characters of the Ceraterpetontidae are:

1. Body elongate.
2. Tail long.
3. Limbs weak; anterior smaller than the posterior.
4. Girdles. Thoracic girdle well developed.
5. Vertebrae strong; spines and chevrons expanded, pectinate.
9. Skull triangular, broad, flattened; nose rounded.
10. Orbits not large, oval; more anterior than in the Urocordylidae.
12. Nares. External nares small, nearly terminal.
13. Lachrymal extends from orbit to naris (in certain restorations).
14. Cornua present.
15. Intertemporal absent.
16. Otic notch absent.

Ceraterpeton (fig. 18*A*, 19*A*) has been placed in the Urocordylidae (Smith-Woodward, Kuhn), Nectridia (Steen), and Ceraterpetontidae (Romer). Its characters are:

9. Skull with posterior edge far behind the articulation for the lower jaw; supratemporal absent or fused with the squamosal; ? double occipital

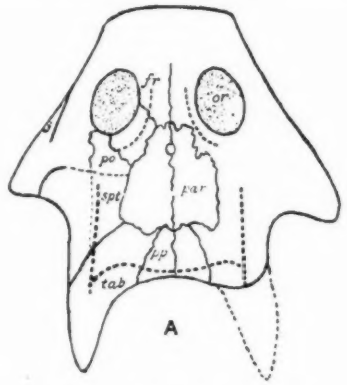

FIG. 18. *Ceraterpeton*. Moodie.

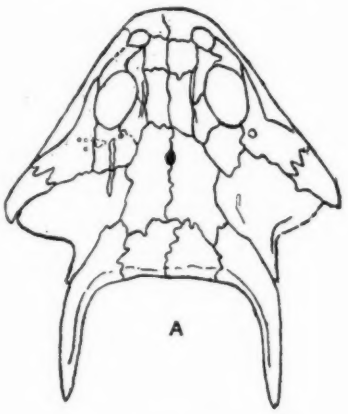

FIG. 19. *Ceraterpeton*. Steen.

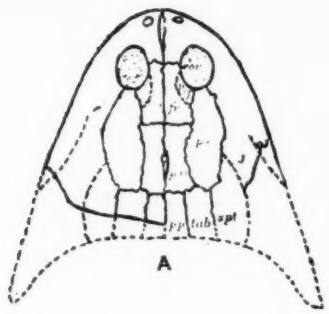

FIG. 20. *Diceratosaurus robustus*. Moodie.

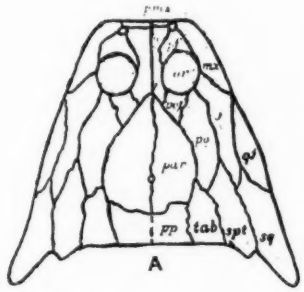

FIG. 21. *Diceratosaurus laevis*. Moodie.

condyle; sensory canals a series of pits tending to develop into grooves with age (increasing size).
10. Orbits oval; in anterior half of the skull.
11. Teeth. A palatal row paralleling the maxillary and premaxillary row.
12. Nares. External nares oblique, oval.
13. Lachrymal extending from orbit to naris.
14. Cornua present; formed of tabular braced by the squamosal.

Diceratosaurus (fig. 20*A*, 21*A*, 22*A*, *B*) was put in the Urocordylidae (Moodie, Smith-Woodward, Kuhn), Ceraterpetontidae (Romer), Pseudocentrophori (Abel). The name *Diceraterpeton* was used by Huene *in errore*. The characters, other than given for the family, are:

9. Skull. The perisquamosal of Jaekel, formed by the combination of the tabular, squamosal, and supratemporal, present; interpterygoid vacuities small; parasphenoid suturally united with the pterygoid.

Eoserpeton (fig. 23*A*) was placed in the Urocordylidae (Moodie, Smith-Woodward, Kuhn) but if, as asserted by Smith-Woodward and Romer, it is synonymous with *Diceratosaurus* it must be placed in the Ceraterpetontidae. The characters are:

1. Body short, stout.
9. Skull triangular, pineal foramen well forward.
10. Orbits oblique, oval; well forward.
12. Nares. External nares small, near the midline, nearly terminal.
14. Cornua long, slender, probably formed by the tabular supported by the squamosal. (Moodie shows the cornua formed by the squamosal probably an error.)
15. Intertemporal absent.
16. Otic notch absent.

DOLICHOSOMATIDAE

This family includes, in the opinion of most authors, the Phlegethontidae, the Molgophidae, and, with the exception of Abel and Romer, the Ophiderpetontidae. The only restoration of the skull of Ophiderpeton is by Steen (1931) and is confessedly capable of other interpretation. The open character of the posterior portion of the skull is much like that of the Dolichosomids and the patch of small scutes over the cheek may well be the impression of a piece of displaced skin.

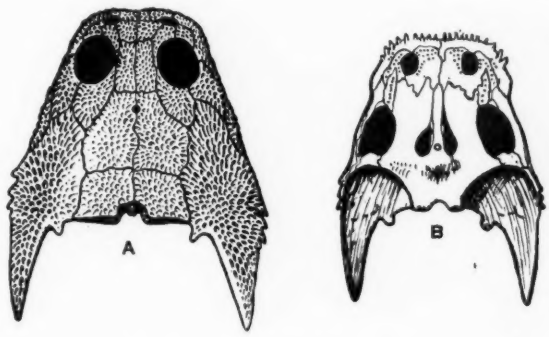

FIG. 22. *Diceratosaurus*. Bystrow.

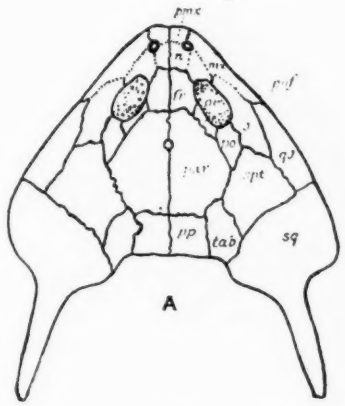

FIG. 23. *Eoserpeton*. Moodie.

	Kuhn	Smith-Woodward	Romer	Steen	Abel	Moodie	Nicholson and Lydekker
Dolichosoma	Dolicho-somatidae	Dolicho-somatidae	Dolicho-somatidae	Dolicho-somatidae	Phlege-thontidae		
Paleosiren	Ophider-petontidae			indet.			Dolicho-somatidae
Phlegethontia	Phlege-thontidae	Dolicho-somatidae	Phlege-thontidae		Phlege-thontidae	Molgoph-idae	
Molgophis	Molgophidae		Phyllospondyli		Molgophidae	Molgophidae	
Ophiderpeton	indet.	Dolicho-somatidae	Ophider-petontidae	Aistopoda	Ophider-petontidae		
Ichthyerpeton	Amphi-bamidae	Labyrinth-odonta				Nyranidae	
Thyrsidium	Dolicho-somatidae	Dolicho-somatidae	Ophider-petontidae		Ophider-petontidae	Ptyonidae	

The table above shows how general, though not unanimous, is the recognition of the Dolichosomatidae, and this becomes rather striking when it is remembered that the Phlegethontodae, the Molgophidae, and perhaps the Ophiderpetontidae are synonymous with the Dolchosomatidae.

The characters of the Dolichosomatidae assembled from the descriptions of the families included above are:

1. Body elongate, serpentiform.
2. Tail (probably) elongate; vertically expanded.
3. Limbs absent, or probably (Molgophidae, Phlegethontidae) absent.
4. Girdles present, or probably (Molgophidae, Phlegethontidae) present.
5. Vertebrae with strong transverse processes.
6. Ribs short, straight, with broad proximal ends and uncinate processes (Ophiderpetontidae); very strong (Molgophidae); reduced or absent (Phlegethontidae); two-headed, slender, with uncinate processes (Dolichosomatidae).
7. Sculpture light or absent.
8. Scutes on abdomen or whole body, long, slender on venter, rounded on dorsum (Ophiderpetontidae), absent (Molgophidae and Dolichosomatidae), unknown (Phlegethontidae).
9. Skull elongate, narrow (Dolichosomatidae, Phlegethontidae); unknown in others.
10. Orbits small, in anterior half of the skull (Ophiderpetontidae); median or post-median (Dolichosomatidae); unknown in others.
11. Teeth erect, cylindrical, dentine not infolded; not swollen at base (Ophiderpetontidae); fine cones (Dolichosomatidae); not known in others.
12. Nares. External nares large, round (Ophiderpetontidae); not known in others.
13. Lachrymal unknown in all.
14. Cornua absent (Dolichosomatidae); unknown in others.
15. Intertemporal unknown in all, probably absent.
16. Otic notch deep in Ophiderpetontidae; unknown in others.

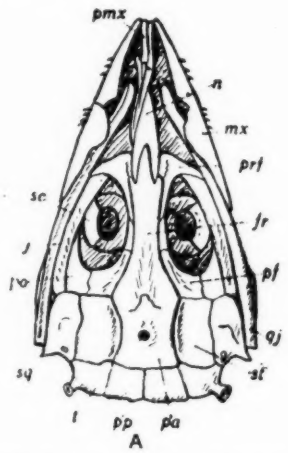

FIG. 24. *Dolichosoma*. Goodrich.

Dolichosoma (fig. 24*A*) was placed in the Dolichosomatidae by all except Abel, who placed it in the Phlegethontidae. *Paleosiren* from the lower Permian of Olivetin (Oëlberg), near Branau, is probably a synonym of *Dolichosoma*. Lydekker (1889) estimated its length at 45 feet. The characters are those given for the family.

Phlegethontia is generally regarded as a synonym of *Dolichosoma*, the absence of ribs in the specimen and the geographical separation are the only objections.

Molgophis is generally regarded as a Dolichosomid, but Romer (1930) regarded it as synonymous with

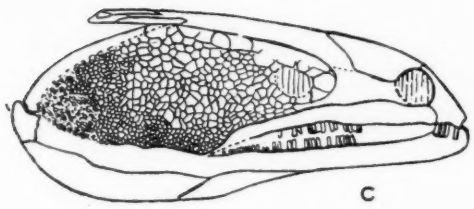

FIG. 25. *Ophiderpeton*. Steen.

Colosteus, which he placed in the Phyllospondyli, a group which he later abandoned. No skull has been referred to this genus but Abel rightly insists that the strong vertebrae with strong lateral ridges and the strong ribs are characters not consistent with its being referred to the Phyllospondyli. It is possible that the two authors were considering different specimens not of the same genus. Kuhn suggested that *Molgophis* is synonymous with *Nummulosaurus*, but this is uncertain as the skull is lacking in both.

Ophiderpeton (fig. 25*C*) is most uncertain. Romer regarded *Oestocephalus*, *Thyrsidium*,and *Ichthyerpeton* as synonyms of *Ophiderpeton*. Steen (1938) regarded the Bohemian specimen referred to *Ophiderpeton* by Fritsch as indeterminate. The characters are those of the family with the exception of the reduction of the cheek bones and the presence of a plaster of scutes, which may be accidents of preservation. The specimen called *Ophiderpeton* by Fritsch and regarded as indeterminate by Steen was called *Steenosaurus* by Kuhn.

Ichthyerpeton is regarded as a synonym of *Ophiderpeton* and so a Dolichosomid.

DIPLOCAULIDAE

This family is accepted by all workers and is generally placed close to the Ceraterpetontidae as part of an evolutionary series. The characters of the family, gathered from various authors, are:

1. Body long, serpentiform, reaching a meter or more in length.
2. Tail vertically expanded, elongate.
3. Limbs very small; humerus with entepicondylar foramen.
4. Girdles. Clavicles and interclavicle large; scapula and coracoid small.
5. Vertebrae long, cylindrical; zygosphene and zygantrum present; neural spines and chevrons heavy, not elongate, rugose (not pectinate).
6. Ribs slender (stout, Williston), double-headed.
7. Sculpture of small pits on skull, clavicles and interclavicle.
8. Scutes absent.
9. Skull triangular, very flat; facial region very abbreviate; prefrontal and nasal absent according to Watson but present according to most authors; postorbital excluded from orbit; interpterygoid vacuities large; occipital condyle double; parasphenoid sutured to pterygoid.
10. Orbits small, far forward.
11. Teeth small conical, large pulp cavity, no infolding of dentine; isodont.
12. Nares. External nares small, terminal.
13. Lachrymal not touching naris.
14. Cornua very large; composed of several bones.
15. Intertemporal absent.
16. Otic notch absent.

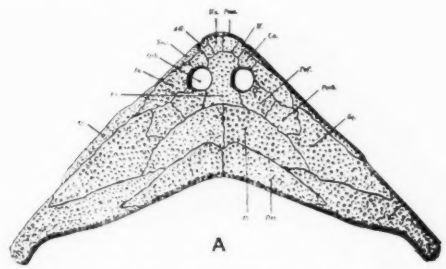

FIG. 26. *Diplocaulus*. Abel.

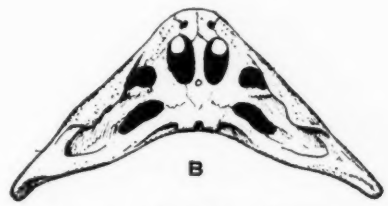

FIG. 27. *Diplocaulus*. Bystrow.

Diplocaulus (fig. 26*A*, 27*B*) is, with the exception of Abel who puts it in the Ceraterpetontidae, placed by all authors in the Diplocaulidae. The characters are those of the family, to which may be added:

9. Skull with complete loss of the nasal, according to Watson.
10. Orbits more anterior and more dorsal than in any related form.
14. Cornua of great size, composed of tabulars, dermosupraoccipitals and squamosals.

Diplocaulus is, in the opinion of all writers, closely connected with the Ceraterpetontidae. It is constantly referred to as the terminal member of a series extending from the Carboniferous into the Permian with increased specialization in the skull and with progressive decadence of the limbs. Romer (1930) says that it was developed from the Ceraterpetontidae but that the characters noted by Watson (1913), the increased size of the cornua, the loss of the nasals, the increased size of the interpterygoid vacuities and the manner of the support of the pterygoid by the parasphenoid demand its being placed in a separate family.

Watson (1913) suggested the series *Caterpeton-Batrachiderpeton-Diplocaulus*. He says,

> In fact the only important difference between the two types (*Batrachiderpeton* and *Diplocaulus*) lies in the palate. *Diplocaulus* differs from *Batrachiderpeton* exactly as does *Eryops* from *Loxomma*.
>
> The dentition in the types are identical in general lines. The differences are that in *Batrachiderpeton* there are large pterygoids meeting in the middle line and supported by the basisphenoid, in *Diplocaulus* there are large interpterygoid vacuities and the pterygoids are supported by the parasphenoid.

Permoplatyops (fig. 28*B*), for *Platyops* of Williston, preoccupied, was placed in the Diplocaulidae (Williston, Hay). Kuhn placed it in the Branchiosauridae which was reserved by him for uncertain forms. Williston based his genus on a specimen called *Diplocaulus pusillus* (Broili 1904), and two specimens in his own collection which he says "show all the essential characters of the Diplocaulidae, but which to unite in the genus *Diplocaulus* is to disregard all taxonomic characters." The characters given by Williston are:

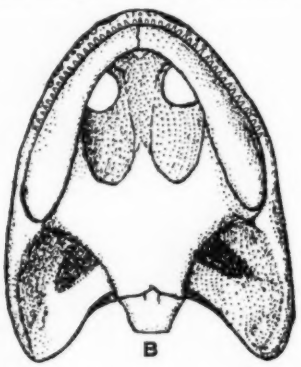

FIG. 28. *Permoplatyops*. Williston.

7. Sculpture like that of *Diplocaulus*.

9. Skull very small, length 22 mm.; sutures of the top "so far as they go agree well with those of *Diplocaulus*." Parasphenoid process incomplete anteriorly; facial region abbreviate; nasals not separate from the premaxillaries; frontals not separated by suture; pineal opening not distinguishable.

10. Orbits far forward.

14. Cornua formed by tabular, short.

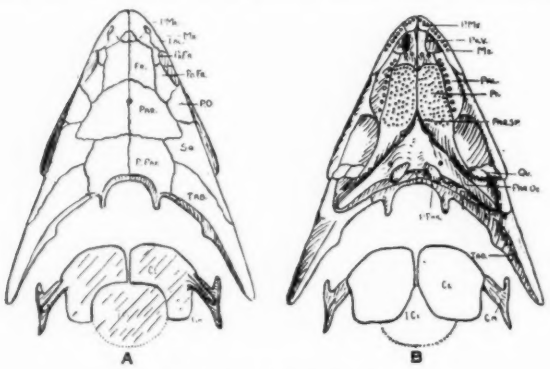

FIG. 29. *Batrachiderpeton*. Watson.

Suggestion has been made that this is an immature *Diplocaulus*. If so, it implies an extraordinary change in the form of the skull with growth.

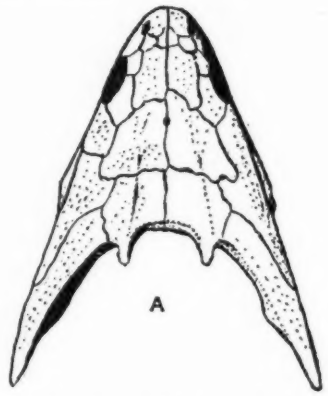

FIG. 30. *Batrachiderpeton*. Bystrow.

Batrachiderpeton (fig. 29*A*, *B*, 30*A*, 31*B*) is placed by all in the Diplocaulidae. The characters are:

9. Skull elongate, triangular, not flattened; interpterygoid vacuities small, nearly closed; parasphenoid process slender; basipterygoid process small, movably articulated to the pterygoid; dermosupraoccipital large; nasals very small.

10. Orbits small, far forward, on the sides of the skull.

11. Teeth. Premaxillary and maxillary teeth isodont; two large teeth on prevomer, nine on the palatine, denticles on pterygoid.

12. Nares. External nares small, nearly terminal.

13. Lachrymal not touching orbit.

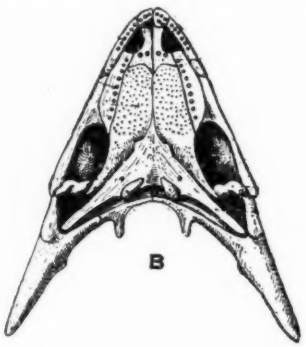

FIG. 31. *Batrachiderpeton*. Abel.

14. Cornua large, formed by tabular, supported by squamosal; small cornua on dermosupraoccipital.
16. Otic notch absent.

According to Watson, the specimen called *Urocordylus reticulatus* by Hancock and Atthey, is synonymous with *Batrachiderpeton* (1913).

Crossotelus is known only from vertebrae, limb bones, and ribs. It was placed in a distinct family, Crossotelidae (Williston), in the Urocordylidae (Kuhn), and in the Ptyonidae (Abel), but so little is known of it that its position is very uncertain. So far as known the characters are:

1. Body slender, perhaps 1 meter in length.
4. Limbs small, ? no foramen in humerus.
5. Vertebrae. Spines short, broad, crenulated, interlocking with those of adjacent vertebrae; zygosphene and zygantrum present.
8. Scutes (or gastralia) abundant and strong.

MICROBRACHIDAE (HYLONOMIDAE)

The family Hylonomidae has been consistently recognized though based on very inadequate material. The genus *Hylonomus* was founded on a mixed lot of bones found in the hollow of a petrified stump in the South Joggins mine, Nova Scotia. The material indicates the existence of an active, lizard-like group of Stegocephalians. The genus *Microbrachis* is so much better known that the family name were better founded on it than on *Hylonomus*. The group or family has so many suggestions of reptilian structure that Dawson named it Microsauria, a name which he unfortunately extended to all the Nova Scotian forms, and Baur long ago summed up the characters and suggested that the reptiles were derived from this group.

The material cited by all authors is so mixed and so incomplete that the family must be thought of rather as convenient than as demonstrated. Only in 1940 was a figure of the skull given by Watson and that was based on the "*Hylonomus*" *geinitzi* of Credner from the Permian locality near Dresden, which may easily be unrelated. In such a family would be included *Hylonomus*, *Hyloplesion* (*Stelliosaurus*), *Microbrachis*, and possibly *Ricnodon*. Numerous genera of uncertain position have been included in this family; Smith-Woodward gives the longest list: *Hylonomus*, *Hyloplesion*, *Hylerpeton*, *Smilerpeton*, *Fritschia*, *Seelya*, *Ricnodon*, *Orthacosta*, *Microbrachis*, *Odonterpeton*, ? *Petrobates*, ? *Limnerpeton*, ? *Dendrerpeton*. The group, whatever name it may bear, is indefinite and may be radically altered with increased knowledge.

Westoll (1943) placed *Hylonomus*, *Microbrachis*, and *Hyloplesion* in the Adelospondyli, basing his action largely upon Steen's (1938) conclusions and Watson's (1940) acceptance of them. Watson refers to these genera as "adelospondylus Microsaurs," a confusing term as the Microsauria is generally considered as equivalent to the Lepospondyli.

As now conceived the characters of the family are:

1. Body long, lizard-like.
2. Tail long, round in section.
3. Limbs well formed; posterior pair larger than the anterior; carpus and tarsus ossified or cartilaginous.
4. Girdles. Clavicles as in *Branchiosaurus;* pubis ossified.
5. Vertebrae with well formed neural spines not crenate.
6. Ribs long, slender, curved, two-headed.
7. Sculpture slight or absent.
8. Scutes of various form on venter and, rarely, dorsum.

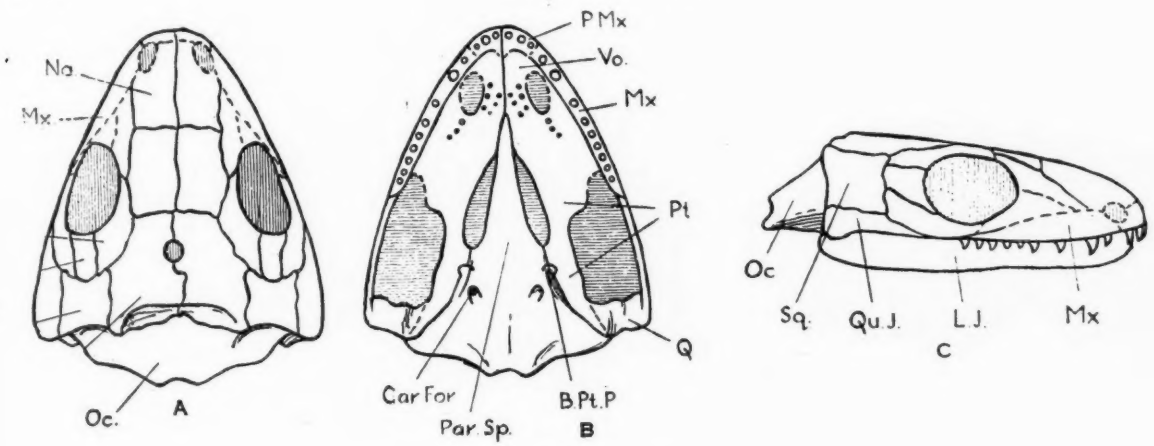

FIG. 32. *Hylonomus*. Watson.

9. Skull slender.
10. Orbits large, in anterior half of the skull, on the upper surface.
11. Teeth conical, dentine not infolded.

Hylonomus (fig. 32*A*, *B*, *C*) is put in the Hylonomidae by most, but in the Microbrachidae (Romer, Steen and ? Abel), and the Branchiosauridae (Kuhn). The characters, in addition to those of the family, are:

3. Limbs. Entepicondylar foramen present in humerus; long axes of the proximal and distal ends of the humerus almost at right angles to each other.
9. Skull. Basipterygoid process of the parasphenoid directed forward; interpterygoid vacuities very large; large smooth bone projecting down and back at posterior edge of the skull; dermosupraoccipital absent.
10. Orbits small and largely lateral; in midlength of the skull.
11. Teeth simple cones, large anteriorly; denticles on the palatine.

Steen regards the specimens from the region of Dresden and from Bohemia as questionable or indeterminate.

Watson's description (1940) of "*Hylonomus*" *geinitzi* from near Dresden has the characters:

5. Vertebrae with long, slender, notochordal centra.
6. Ribs long, slender, slightly curved, single-headed.
9. Skull small, triangular, massive, "appears to have been fairly elevated"; occipital region projects considerably behind posterior edge of the surface, this region is smooth and projects down at an angle and is continuous with the widely expanded posterior portion of the parasphenoid; "I think quite certainly" (Watson) no tabular or supratemporal; basipterygoid processes short; process of parasphenoid wide, powerful; interpterygoid vacuities narrow.
10. Orbits small, midlength of skull, separated.
11. Teeth on jaws a rather irregular series, short, stumpy, blunt; small teeth on palatines and prevomers; palatine covered with small pits, "perhaps for denticles" (Watson).

Hyloplesion (fig. 33*A*, *B*), originally described by Fritsch as *Stelliosaurus* (preoccupied); was placed in the Hylonomidae (Smith-Woodward, Kuhn) and with question in the Adelospondyli (Steen). She says (1938) and is quoted with approval by Watson (1940) and Westoll (1943), that the marked similarity of skull structure in *Microbrachis* and *Hyloplesion* indicates that the latter is an Adelospondylid; it was regarded as a synonym of *Hylonomus* (Credner, Broili) but this is denied (Steen). The characters are:

3. Limbs well formed, the posterior the larger; carpus and tarsus ossified.
9. Skull elongate, parietal large; parasphenoid articulated moveably to the pterygoid; posterior part of the parasphenoid small; prevomer long broad; interpterygoid vacuities small.
10. Orbits oval, large, lateral, in anterior half of the skull.
11. Teeth in premaxillary and maxillary small, conical, dentine not infolded; denticles on all palatal bones, no enlarged teeth.
12. Nares. External nares, oval, oblique, nearly terminal.
14. Cornua absent.
15. Intertemporal absent.
16. Otic notch absent.

MICROBRACHIDAE

This family from the Permian of Bohemia is the adaptive equivalent of the Hylonomidae from Nova Scotia, if not, indeed, the same family. The characters are almost the same as those of the Hylonomidae.

1. Body small, slender, lizard-like.
3. Limbs. Anterior pair very small.
4. Girdles. Interclavicle broad with serrate edges and long process.
5. Vertebrae. Notochordal space large; spines thin.
6. Ribs stout (Lydekker) or thin (Fritsch).
7. Sculpture strong on the skull.
8. Scutes cover whole body (Lydekker), or abdomen only (Fritsch).
9. Skull high; posterior edge concave; no posterior plate.
10. Orbits oval, far forward, on sides of skull.
11. Teeth. Large pulp cavity, dentine infolded only at top; small teeth in parallel rows on pterygoid and parasphenoid.
12. Nares. External nares small, anterior, not terminal.

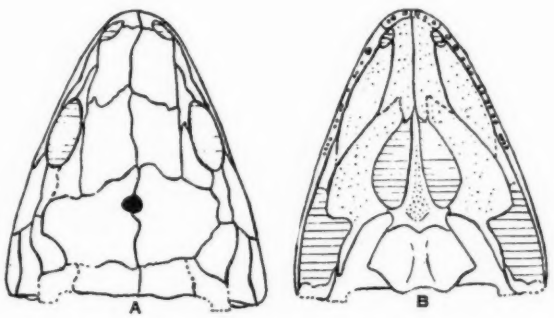

FIG. 33. *Hyloplesion*. Steen.

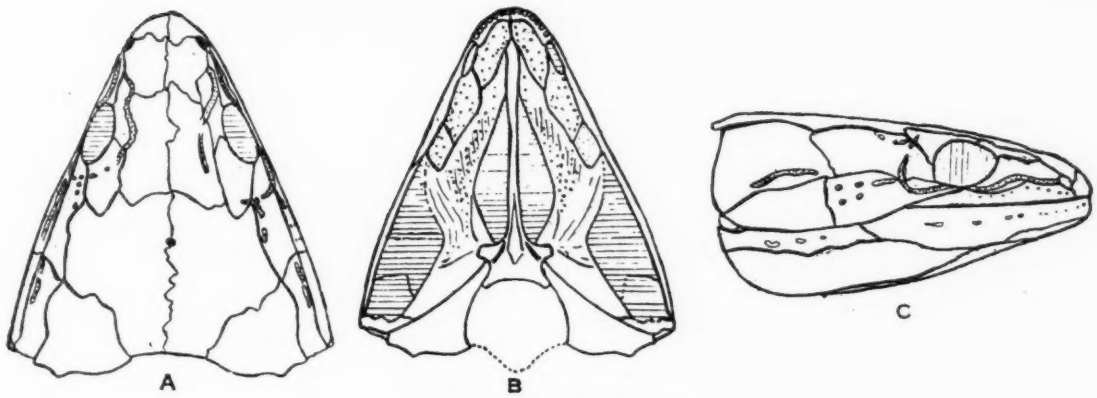

FIG. 34. *Microbrachis*. Steen.

13. Lachrymal extends from orbit to naris.
16. Otic notch absent.

Microbrachis (fig. 34*A*, *B*, *C*) was placed in the Hylonomidae (Smith-Woodward), Microbrachidae (Lydekker), Gastrocentrophori (Abel), Adelospondyli or ? (Steen), Branchiosauridae (Kuhn). *Ricnodon cf. dispersus* was regarded as a synonym of Microbrachis (Steen). Its characters are:

7. Sculpture ranging from smooth to close dichotomizing lines with age (large size).
8. Skull high; posterior edge concave; squamosal, supratemporal and tabular united (Jaekel's perisquamosal); parasphenoid with small body, movably articulated to the pterygoid; basisphenoid (basioccipital of Steen) large, firmly united to parasphenoid; interpterygoid vacuities small; sensory canals disappeared with age (large size); dermosupraoccipital small and on upper surface in young (small size) or on posterior face in age (large size).
10. Orbits oval, far forward, on sides of skull.
11. Teeth in rows on pterygoid and palatine; denticles on palatal bones.
12. Nares. External nares small, anterior, not terminal; internal nares oval, elongate, lateral.
13. Lachrymal extends from orbit to naris.
16. Otic notch absent.

Ricnodon (fig. 35*A*, *B*, 36*A*) was placed in the Hylonomidae (Smith-Woodward, Hummel), Branchiosauridae (Kuhn), and *incertae sedis* by Steen (1938) who considered it as probably a synonym of *Microbrachis pelekani;* she says "presumably a Lepospondyl." Its characters are:

5. Vertebrae "appear to show" coössified centra and neural arch.
9. Skull triangular, nose rounded; posterior edge broad, nearly straight; interfrontal present; either no supratemporal or a united supratemporal and tabular present; body of parasphenoid broad, process coming to a point anteriorly.
10. Orbits large, round, midlength of skull.
11. Teeth present on premaxillary, absent on maxillary; denticles on all palatal bones; in rows on palatine, pterygoid, and ectopterygoid.
12. Nares. External nares small, oval, oblique; relatively separated. Internal nares large, lateral.
13. Lachrymal extends from orbit to naris.
14. Cornua minute.

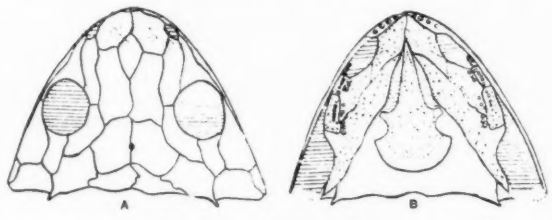

FIG. 35. *Ricnodon*. Steen.

UROCORDYLIDAE

This family contains most of the genera of the abandoned Ptyonidae and Tuditanidae. It is close

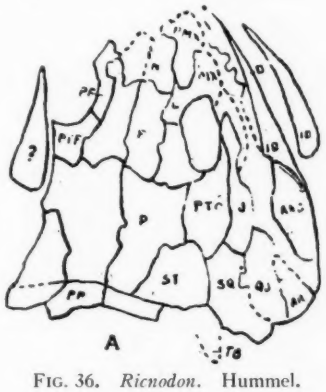

FIG. 36. *Ricnodon*. Hummel.

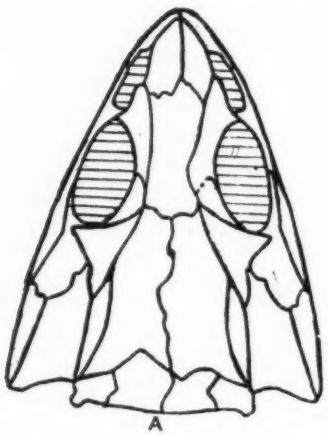

FIG. 37. *Urocordylus*. Steen.

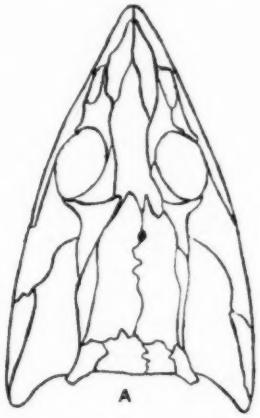

FIG. 38. *Urocordylus*. Steen.

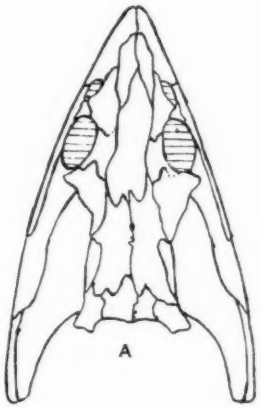

FIG. 39. *Urocordylus*. Steen.

to the Dolichosomatidae on the one hand and to the Ceraterpetontidae on the other; the members of the family have better developed limbs, a less slender skull than the Dolichosomatidae, and differ from the Ceraterpetontidae by stronger limbs, weak cornua, and the presence of an otic notch. It differs from both families in the weak development of the dermal scutes. It is apparent that the Dolichosomatidae and the Ceraterpetontidae had abandoned the crawling habit of the Amphibamidae and taken to swimming by bodily motion rather than by use of the limbs; the Urocordylidae were approaching this condition and exhibit a specialization in the large size and peculiar ornamentation (pectination, granulation) of the neural spines and chevrons. In these characters they were approached by *Diplocaulus* and *Crossotelos*. The characters of the Urocordylidae are:

1. Body elongate.
2. Tail flattened vertically, deep and strong; 80 vertebrae.
3. Limbs of moderate size.
4. Girdles. Thoracic moderately developed; interclavicle shield-shaped.
5. Vertebrae. Spines and chevrons high, wide, and pectinate.
6. Ribs long, strong, two-headed.
7. Sculpture weak or absent.
8. Scutes generally weak, oat-shaped, confined to abdominal surface.
9. Skull triangular, snout round or pointed; truncate posteriorly.
10. Orbits far forward, oval, separated.
11. Teeth slender, pointed, recurved, large pulp cavity, no infolding of the dentine; denticles on parasphenoid and pterygoid.
12. Nares. External nares elongate, oval, or very elongate.
14. Cornua small, "aborted."
15. Intertemporal absent.
16. Otic notch present.

Urocordylus (fig. 37*A*, 38*A*, 39*A*) has been placed in the Urocordylidae (Smith-Woodward, Kuhn), Nectridia (Steen), Ptyonidae (Abel). Smith-Woodward considered *Oestocephalus* and *Ctenerpeton* as synonyms of *Urocordylus*, and Watson said that *Urocordylus* probably belongs with *Ceraterpeton*. The characters are those of the family, with some addition for the skull.

9. Frontal single; supratemporal small, long, narrow; no trace of sensory canals; interpterygoid vacuities small; prevomer long and slender.

Ctenerpeton is known only from the axial skeleton. It has been placed with little certainty in various families. *Sauropleura remex* and *Oestocephalus remex* have been considered as synonyms (Romer 1930, Steen 1930). The elongate, pectinate spines would place it in the Urocordylidae. It is indeterminate as a genus.

Lepterpeton is known only from a poor skull and a lower jaw. It has been placed in the Urocordylidae (Smith-Woodward, Kuhn) and the Ptyonidae (Abel). A doubtful specimen from the Westphalian of Nyran, Bohemia, placed in this genus is regarded by Steen (1938) as indeterminate.

Scincosaurus (fig. 40*A*, *B*) is placed in the Urocordylidae (Smith-Woodward, Steen, Kuhn), and *incertae sedis* (Abel). Kuhn regarded it as a synonym of *Ceraterpeton*, but Steen (1938) restored it to an independent position. The characters given by Steen are:

9. Skull lacking supratemporal, intertemporal, dermosupraoccipital, and tabular; postorbital ? present; ectopterygoid absent; parasphenoid with wide body and short process, movably

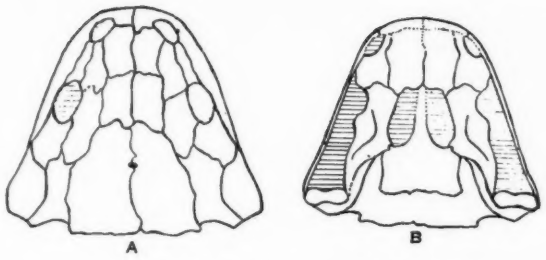

FIG. 40. *Scincosaurus*. Steen.

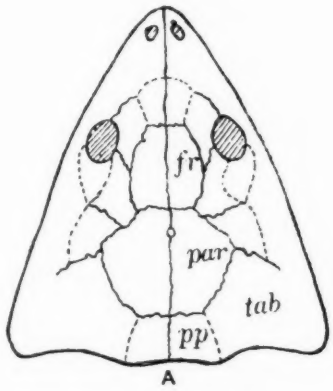

FIG. 41. *Tuditanus*. Moodie.

articulated to the pterygoid; interpterygoid vacuities small, oval; palatine entirely anterior to the pterygoid; basioccipital present.

Ptyonius and *Tuditanus* (fig. 41*A*, 42*A*) are regarded by practically all as composed of synonymous forms or indeterminate specimens. Romer regarded *Ptyonius* (1930) as belonging in the Colosteidae (Sauropleuridae) which he considered a family of the Phyllospondyli, but as he afterward rejected the Phyllospondyli the genus becomes indeterminate. *Isodectes* (fig. 43*A*, *C*) is a synonym of *Tuditanus* according to Romer.

COLOSTEIDAE (SAUROPLEURIDAE)

All members of this family are from the Allegheny Formation, Pennsylvanian, of Linton, Ohio. A large number of specimens have been referred to it which are now regarded as synonymous or indeterminate. The families must be regarded as indeterminate because a list of the characters could be adjusted to several other families. The following list of the various genera, usually included, will illustrate the confusion.

Colosteus was placed in the Urocordylidae (Smith-Woodward, Kuhn), Phyllospondyli (Romer, Steen), ? Labyrinthodontia (Romer). Romer (1930) listed nine genera, certain specimens of which he regarded as synonyms of *Colosteus acutus;* Steen (1930) rejected two of these—"highly improbable" that *Molgophis* and *Pleuropteryx* can be assigned to *Colosteus*. Romer (1930) put *Colosteus* in the Phyllospondyli as "Branchiosaurs of a peculiar type," and "aberrant but primitive Branchiosaurs." In 1938 he suggested that *Colosteus* might be a Labyrinthodont as it is "obviously related to *Erpetosaurus*." There are two points cited in the description which are inconsistent. The vertebrae are often unossified, suggesting the Phyllospondyli, and the ribs are "too long and curved for a Branchiosaur." If *Colosteus* is a Branchiosaur and if there are no Phyllospondyli, the resting place, so far, is in the Labyrinthodontia near *Ereptosaurus*.

The name *Sauropleura* (fig. 44*A*, 45*A*, 46*C*, 47*A*) has precedence over *Colosteus* and must go the same way. Romer lists species of five genera as synonyms, and Steen and Smith-Woodward each add one, making seven in all.

Odonterpeton is put in the Branchiosauridae (Kuhn), Tuditanidae (Moodie), Colosteidae, as it is a synonym of *Erpetosaurus* (Romer 1930), but *Colosteus* is put in the ? Labyrinthodontia later by Romer (1938) as it is obviously related to *Erpetosaurus*. The last analysis places it in some family of the Rhachitomi.

Pygopterus (of Newberry) is a synonym of *Sauropleura* (*Colosteus*) according to Romer (1930).

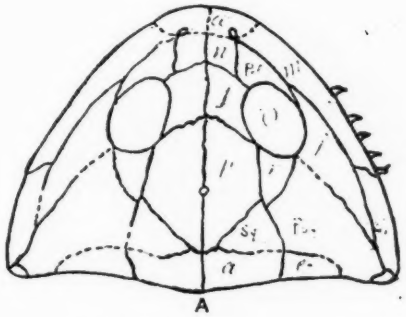

FIG. 42. *Tuditanus*. Moodie.

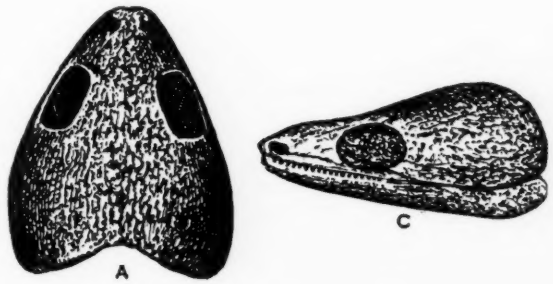

FIG. 43. *Isodectes*. Williston.

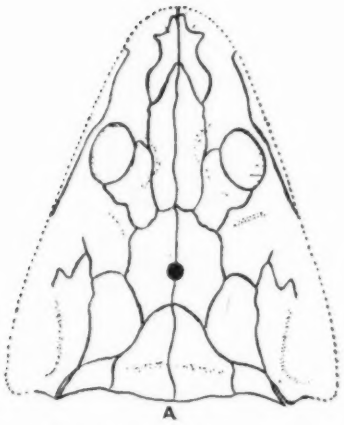

FIG. 44. *Sauropleura*. Steen.

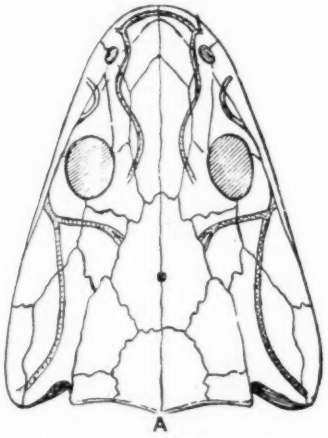

FIG. 45. *Sauropleura*. Romer.

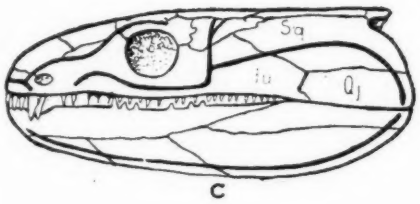

FIG. 46. *Sauropleura*. Bystrow.

LIMNERPETIDAE (LIMNERPETΩNTIDAE)

This proposed family has been shown to be an assemblage of unrelated and indeterminate forms by Steen (1938).

Limnerpeton has been shown by Steen to be indeterminate.

Microdon, preoccupied, is a synonym of *Lepterpeton*.

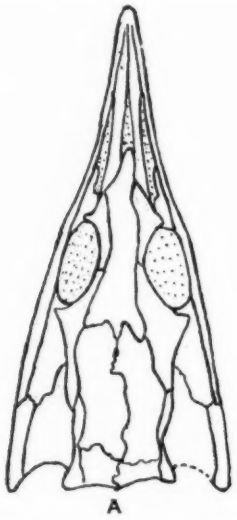

FIG. 47. *Sauropleura*. Steen.

EMBOLOMERI

The way to an understanding of the structure and significance of the Ichthyostegalia was pointed out in Watson's papers on the Amphibia, especially the Croonian Lecture on the "Evolution and Origin of the Amphibia," 1925, and "The Carboniferous Amphibia of Scotland." The appearance of the last paper in the *Paleontologica Hungarica* was much delayed, and various dates have been given for its publication but in a footnote on page 881 of Steen's paper on the "Amphibia from Linton, Ohio," 1930, Watson states that it was set up in type in 1923, some proof sheets were possibly circulated in 1926, but the first distribution to libraries was in 1929 and more extensively in 1930. It is apparent that though the date of publication is properly 1929, as accepted by Watson, he had committed to manuscript his ideas of the phylogenetic and taxonomic position of the Embolomeri by 1923, at least. The suggestion that the rhachitomous vertebrae were derived from the embolomerous type by a process of chondrification, rather than a building up of the embolomerous from rhachitomous by increasing ossification as previously supposed, was made by Williston in his study of *Trimerorhachis*, but Watson's studies of the Carboniferous forms furnished the proof that the Embolomeri were both older and more primitive, in the sense of retaining ancestral characters, than the Rhachitomi. The later discovery of the Ichthyostegalia, even older and more primitive, helped close the gap between the Stegocephalia and the Crossopterygia and made more evident the probable path of evolution. Evidence drawn from morphological characters, even when supported by proper sequence in time, can only produce an approximation to proof, but the accumulation of such evidence may become so weighty as to warrant positive conclusions. In this way the broad lines of the evolution of the Stegocephalia have become as well established as those of any other line of the vertebrates.

How radical is the change in our conception of the course of evolution in these forms is illustrated by Watson's remark (1926) that "at any given period the members of these two orders (Phyllospondyli and Lepospondyli) are of more advanced structure than the Labyrinthodonts." That evolution was not uni-

form in rate or direction is shown by the difference in degree of advance from the primitive and in the fate which Säve-Söderberg affirms for the Anthracosauroideae and the Loxommoideae, the first leading to the Reptilia and the second to the younger Amphibia, under the influence of what he calls "evolutionary trends expressing a vital quality in the genotype." He says (1934) that the Loxommoideae are comparable to the Ichthyostegids and may well have originated from them, which is also true of the Rhachitomi, Stereospondyli, and Phyllospondyli, but that the Anthracosauroideae of Watson are not in this line but form an Order, the Anthracosauria (of Säve-Söderberg), which led to the reptiles, birds, and mammals. These two groups are his Batrachomorpha and Reptiliomorpha. His suggestion has not been generally accepted.

The term Labyrinthodonta was defined by Watson as including the Embolomeri, Rhachitomi, and Stereospondyli, as opposed to the other groups of the Amphibia. Säve-Söderberg further restricted the term by excluding the Anthracosauroidei (Anthracosauria of Säve-Söderberg). He says (1935) the Loxommids are "clearly and nearly" related to the Ichthyostegids and may be considered as descendants from a primitive Ichthyostegid. The Anthracosaurids differ in many and important characters from the Loxommids and the Ichthyostegids and cannot be derived from the Ichthyostegids. They may even have arisen from fish independent of the Loxommids and Ichthyostegids. He believed that the two groups of Embolomeri had parted ways as early as the Devonian, one leading to the younger amphibians and the other to the reptiles, birds, and mammals. He goes so far as to assert (1935) that the Labyrinthodontia, in his sense, were polyphyletic. The "Rhachitomi" and "Stereospondyli" he regarded as merely phases which might appear in any group. "Each of them includes representatives of several lines of evolution; accordingly each such line may include both rhachitomous and stereospondylus members."

Säve-Söderberg in his final separation of the Anthracosauria from the Embolomeri as a distinct Order (1935) says that the Anthracosaurids are less related to the Loxommids and the Ichthyostegids than these are to each other. The Anthracosaurids are more primitive and fish-like in many characters than are the Ichthyostegids and evidently separated from the line of descent of the Ichthyostegids very early. Watson's Embolomeri is therefore not a unit group; the Anthracosauria is an independent line of embolomerous forms probably belonging to the line leading from the fish ancestor of the Tetrapods to the Reptilia. The Loxommidae are the only Carboniferous Stegocephalia—in the same line as the later Labyrinthodonts—hence his Order Loxommoidei. The Labyrinthodontia, *sens. st.*, consists of Loxommoidei, "Rhachitomi"-Stereospondyli-Phyllospondyli-? Anura (= Batrachomorpha).

Watson's definition of the Labyrinthodonta and his Grade Embolomeri (1929) is as follows:

Order Labyrinthodontia Owen

Amphibia with a completely roofed skull, a lower jaw with a prearticular and more than one coronoid in addition to the usual bones. Vertebrae composed of separate neural arches and intercentra with pleurocentra in addition in most forms.

Grade Embolomeri Cope

Labyrinthodonts with a single occipital condyle which may be purely on the basioccipital or may extend to the exoccipitals, but is always nearly circular and concave and composed mainly of the basioccipital. An ossified basioccipital and supraoccipital always present. Dermosupra-occipitals and tabulars not provided with any occipital flanges attached to the hinder surface of the otic region of the neural cranium. A horn or process from the hinder edge of the tabular which is associated with the attachment of the shoulder girdle always present. Pterygoids supported by a moveable articulation with the basipterygoid process and with a very large palatal part, so that the interpterygoid vacuity is small and the two pterygoids meet in a symphysis. Vertebrae composed of neural arches, pleurocentra and intercentra, the last two elements being similar in size and forming complete rings round the notochord. Presacral, and sometimes the sacral ribs, double-headed.

The classifications of Watson and Smith-Woodward are fairly concordant.

Watson, 1926	Smith-Woodward, 1932
Embolomeri	Embolomeri
Anthracosauroideae	
Eogyrinidae	Anthracosauridae
Eogyrinus	*Anthracosaurus*
Pholiderpeton	*Pteroplax*
Eobaphetes	*Otocratia*
Macrerpeton	*Paleogyrinus*
Anthracosaurus	*Eogyrinus*
Paleogyrinidae	*Pholiderpeton*
Paleogyrinus	*Diplovertebron* (*Gephyrostegus*)
Pteroplax	? *Nummulosaurus*
Otocratidae	*Eobaphetes* (*Erpetosuchus*)
Otocratia	? *Ichthyerpeton*
Cricotidae	? *Crassigyrinus*
Cricotus	Loxommidae
Pholidogaster	*Loxomma* (*Mioganodus*, *Megalocephalus*, *Orthosaurus*)
Crassigyrinus	*Baphetes*
Diplovertebron (*Gephyrostegus*)	*Macrerpeton*
Macromerion	*Spathiocephalus*
Loxommoideae	Pholidogasteridae
Loxommidae	*Pholidogaster*
Loxomma	Cricotidae
Baphetes	*Cricotus*
Orthosaurus	*Cricotillus*
Spathiocephalus	? *Spondylerpeton*
	? *Macromerion*
	? *Leptophractus*

Watson's definition of the Anthracosauroideae (1929) is as follows:

Embolomeri, with the orbits small, close together and in the middle of the length of the skull. No post-temporal fossae, the whole of the dorsal surface of the otic region of

the neural cranium being in contact with the skull roof. Tabulars produced into long horns, usually with indications of the attachment of the post-temporal. Prevomers small and toothless, the internal nares being large, very anterior in position and not widely separated. Transverse bearing a series of teeth.

His description of the Loxommoideae (1929) is as follows:

Embolomeri in which the small and rounded orbits are continuous with a large triangular vacuity, stretching forward into the lachrymal. The true orbits lie close to the middle line, usually behind the middle length of the skull.

Prevomers of medium or large size, each bearing a pair of alternative tusks. Internal nares small and very widely separated.

Palatine and transverse bones each with a pair of alternative tusks. Tabulars without the long horns found in the *Anthracosauroideae*, but with a small process for the attachment of muscles. A large posttemporal fossa present.

To these definitions Säve-Söderberg (1933) added several explanatory points:

In the Loxommids the squamosal is sutured to supratemporal-intertemporal. In some of the Anthracosauroideae, at least, the attachment of the squamosal is by ligament.

There is never an intertemporal in the true Labyrinthodonts; the bone so-called is a dermosphenotic. Fusion of the supratemporal and the intertemporal took place as early as the transition of the Fish ancestor to the Ichthyostegids. The same is true of the sutural attachment of the squamosal to the supratemporal-intertemporal in the Loxommids.

In the Loxommids the lachrymal is fused with the maxillary.

Some, or all of the Loxommids retained the last remnant of the preopercular. There is no trace of this bone in the Anthracosaurids.

The palate of the Loxommids has large, tooth-bearing prevomers, and large internal nares located near the anterior end of the snout and widely separated. The palate of the Anthracosaurids have long, narrow, toothless prevomers, and large internal nares, near the anterior end of the snout and close together. In the characters of the palate the Loxommids agree with Ichthyostegids and the Anthracosaurids agree with the Seymourids which are upon the line towards the reptiles.

Säve-Söderberg (1935) further distinguished between the Anthracosaurids and the Loxommids-Ichthyostegids as follows:

To summarize, the pattern on the dermal bones on the posterior part of the dermal roof, the structure of the anterior parts of the palate, and the looser attachment of the cheek, clearly indicate that the Anthracosauroids are much less related to the Loxommids and Ichthyostegids than these two groups to each other.[8]

[8] Säve-Söderberg's interpretation of the posterior portion of the skull roof is explained and illustrated in his 1935 paper "On the dermal bones of the head in Labyrinthodont Stegocephalia."

How far Säve-Söderberg's conclusions and his terminology of the bones may become currently accepted is uncertain; as yet they have not found favor with most workers. It is evident, however, that Watson's recognition of the significant difference between the Anthracosaurids and the Loxommids is nearer to the present general opinion than the arrangement by Smith-Woodward and his classification will be followed in this paper.

List Showing the Classification, Geological Horizon, and Location of the Determinable Embolomeri

Anthracosauroideae
- Eogyrinidae
  - *Eogyrinus*, Lower Coal Measures, Westphalian, of Staffordshire, England.
  - *Macrerpeton*, Middle Carboniferous, Allegheny Formation, of Linton, Ohio, U.S.A.
  - *Pholidogaster*, Lower Middle Coal Measures, Westphalian, of Yorkshire, England.
  - *Anthracosaurus*, Lower Coal Measures, Lanarkian, Lancashire, England.
  - *Eobaphetes*, Carboniferous, Washington County, Kansas, U.S.A.
- Paleogyrinidae
  - *Paleogyrinus*, Lower Coal Measures, Lanarkian, of Fifeshire, Scotland.
  - *Pteroplax*, Lower Coal Measures, of Northumberland, England.
  - *Otocratia*, Lower Carboniferous, Mississippian, of Midlothian, Scotland.
- Cricotidae
  - *Cricotus*, Lower Permian, Wichita, of Texas, U.S.A.
  - ? *Cricotillus*, Lower Permian, of Oklahoma, U.S.A.
  - ? *Chenoprosopus*, Lower Permian, of New Mexico, U.S.A.
  - ? *Archeria*, Lower Permian, Wichita, of Texas.
  - *Leptophractus*, Middle Carboniferous, Allegheny Formation, of Linton, Ohio, U.S.A.
  - *Pholiderpeton*, Lower Carboniferous, Mississippian, from near Edinburgh, Midlothian, Scotland.
  - "*Macromerium*," Westphalian, of Nyran, and Stephanian, of Kuonova, Czechoslovakia.
  - *Diplovertebron*, Westphalian, of Nyran, Czechoslovakia.
  - *Crassigyrinus*, Lower Carboniferous, Mississippian, of Midlothian, Scotland.

Loxommoideae
- Loxommidae
  - *Loxomma*, Lower Coal Measures, Lanarkian, of Lanarkshire and Lower Carboniferous, Mississippian, Midlothian, Scotland;
    Questionably, Middle Carboniferous, Allegheny Formation, of Linton, Ohio, U.S.A.

Questionably, Westphalian, of Nyran, Czechoslovakia.

Orthosauriscus (*Orthosaurus*), Lower Coal Measures, Westphalian, Northumberland, England;
Middle Coal Measures, Westphalian, of Lanarkshire and Fifeshire, Scotland;
Middle Coal Measures, Westphalian, of Staffordshire, England.

Spathiocephalus, Lower Carboniferous, Mississippian (Watson (1929) says Lower Carboniferous of Scotland is "certainly Mississippian, probably Tournosian"), of Midlothian, Scotland.

Baphetes, Middle Coal Measures, Westphalian, Lancashire, England;
Questionably, Coal Measures, of Pictou, Nova Scotia.

Dendrerpetontidae

Dendrerpeton, Carboniferous, of South Joggins, Nova Scotia.

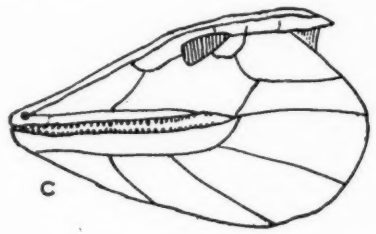

FIG. 48. *Eogyrinus*. Watson.

ANTHRACOSAUROIDEAE

EOGYRINIDAE

The characters are:

9. Skull moderately slender anteriorly; edge of the pterygoid reaches below the articular edge of the quadratojugal.
14. Cornua formed of tabulars; no facet for the posttemporal.

Eogyrinus (fig. 48*C*) has, according to Watson, many synonyms, as:

Anthracosaurus, Hancock and Atthey, *non* Huxley.
Pteroplax, Hancock and Atthey, *in errore*.
? *Strepsodontosaurus*, Barkas.
? *Leptognathus*, Barkas.
? *Macrosaurus*, Barkas.
? *Loxomma*, Embleton, *in errore*.

The characters are:

1. Body very long with a circular section; head small.
2. Tail vertically expanded, very long.
3. Limbs short and feeble.
4. Girdle like *Osteolepis*.
9. Skull. Upper edge of squamosal articulates with and is attached by ligament to the lower surface of the supratemporal. In *Osteolepis* these bones are separated by the spiracular cleft; in later amphibians the bones are united by suture.
10. Orbits small, near the midline of the skull and at midlength.
11. Teeth present on ectopterygoid, absent on prevomer.
12. Nares. Internal nares very large, anterior and not widely separated.
14. Cornua formed by tabular, short and slender.
15. Intertemporal present.

It is interesting that in the collection of the Museum of Paleontology in the University of Michigan there are two specimens of the top of the skull of *Cricotus* that agree in all particulars with the figure of the top of the skull of *Eogyrinus* given by Watson (1925).

Macrerpeton (fig. 49*A*, *B*, *C*) was based by Moodie (1916) on the specimen called *Tuditanus huxleyi* by

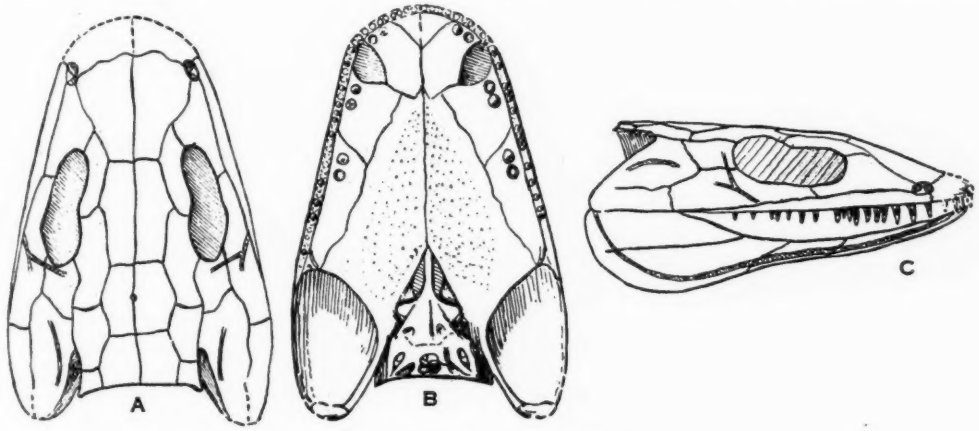

FIG. 49. *Macrerpeton*. Watson.

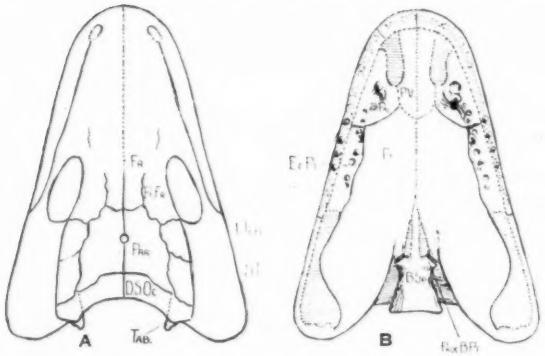

FIG. 50. *Pholidogaster*. Watson.

Cope. Watson placed it in the Anthracosauroideae but with some uncertainty; he said (1929) that the "types are fragmentary skulls and lower jaws. . . ." The animal is "really undeterminable," but "certainly is an Anthracosaurid and probably an Eogyrinid." Säve-Söderberg (1935) said that Watson was in error, that it is a Loxommid. Romer's figures (1930) certainly show Loxommid characters and the genus is discussed under that group.

Pholidogaster (fig. 50*A*, *B*) is placed by all in or near the Eogyrinidae. Its characters are:

7. Scutes present on the venter.
9. Skull broad as long, triangular; interpterygoid vacuities small; pterygoids meet in a suture anteriorly.
10. Orbits, small median.
11. Teeth. Maxillary teeth isodont, cylindrical, apex blunt, somewhat recurved resembling those of *Cricotus;* three anterior maxillary teeth larger than the others; tusks on palatine and ectopterygoid, no teeth on prevomer.
12. Nares. Internal nares large.
14. Cornua not preserved. Watson restores the tabular with long and slender cornua.
16. Otic notch deep.

Anthracosaurus (fig. 51*B*), of Huxley not of Hancock and Atthey, is placed in the Eogyrinidae by all. The characters as given by Watson (1929) are:

9. Skull longer than broad, snout blunt; largest of the Embolomeres, skull 15″ long; occipital condyle single, concave; exoccipitals form sides of brain case and project beyond posterior edge; interpterygoid vacuities small; prevomer narrow; basipterygoid processes massive and carry two pits, for the pterygoid and epipterygoid.
10. Orbits small, near midline and midlength of skull.
11. Teeth round or oval, compressed to two sharp edges at apex; tusks on the ectopterygoid and palatine; premaxillary and first maxillary teeth large.
14. Cornua formed by tabular, massive, great development for attachment of the shoulder girdle.

Eobaphetes was placed in the Eogyrinidae by Watson because of its close resemblance to *Eogyrinus;* it was placed in the Anthracosauridae (Smith-Woodward, Moodie), Cricotidae (Kuhn). The name was proposed by Moodie to replace *Erpetosuchus*, preoccupied, and Kuhn regarded it as a synonym of *Leptophractus*. The specimen consists of an imperfect maxillary, a lower jaw, and fragments of two ribs. Such characters as can be made out from Moodie's (1916) description are:

6. Ribs solid, heavy, curved.
7. Sculpture elongate pits and ridges.
11. Teeth isodont, rather short, bluntly conical, recurved; coarsely striate (dentine infolded).

The figure of the lower jaw given by Moodie shows all the characters of the jaw of *Cricotus*.

PALEOGYRINIDAE

The characters are:

9. Skull with a very short maxillary; edge of the pterygoid extending below the level of the basis cranii.
10. Orbits large.
14. Cornua formed by tabular, long, slender, with a striated facet for the posttemporal.

Paleogyrinus (fig. 52*A*, *C*) was placed in the Anthracosauridae (Smith-Woodward) and in the Paleogyrinidae (Watson, Kuhn). The characters are (Watson 1926):

9. Skull with occipital condyle single, concave, tripartite; supraoccipital ossified; basisphenoid

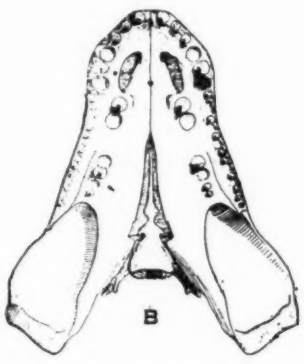

FIG. 51. *Anthracosaurus*. Watson.

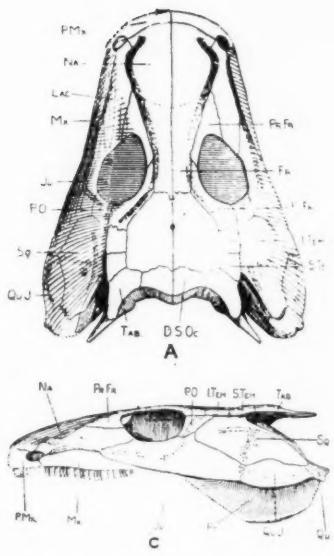

FIG. 52. *Paleogyrinus*. Watson.

and parasphenoid fused; parasphenoid movably articulated to the pterygoid; pterygoids broad, meeting in the midline; interpterygoid vacuities small; a descending process on the quadrate process of the pterygoid; fenestra ovalis represented by a pit only; sensory canals obvious.

10. Orbits large, midlength of skull; angulate contour in front.
11. Teeth so far as known isodont, small, close set, circular section; sharp pointed; not striate (without infolding of dentine).
12. Nares. External nares lateral, near edge.
14. Cornua formed by tabular, ? facet for the post-temporal.
15. Intertemporal present.
16. Otic notch deep.

Pteroplax (fig. 53*B*) has been variously referred. A distinction is made between the two species. *P.*

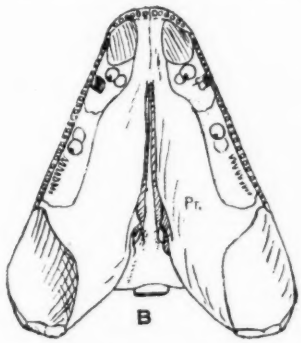

FIG. 53. *Pteroplax*. Watson.

brevicornis was considered as a synonym of *Orthosaurus* and placed in the Loxommidae (Kuhn). *P. cornutus* was considered as a synonym of *Eogyrinus* (Kuhn). It was placed in the Anthracosauridae (Smith-Woodward) and in the Paleogyrinidae (Watson) as the terminal member of a series, *Orthosauriscus* (*Orthosaurus*)-*Eogyrinus-Pteroplax*. The single specimen is a skull table showing some of the features of the lower surface. The characters are:

9. Skull triangular, nose blunt, pterygoids large; interpterygoid vacuities small; occipital condyle single; basi- (or para-) sphenoid articulated movably to the pterygoid; ectopterygoid not shown as present in the figures.
10. Orbits probably of considerable size (indicated by Watson's figure).
11. Teeth. Tusks on prevomers and palatines; denticles on pterygoid.
12. Nares. Internal nares large, lateral.

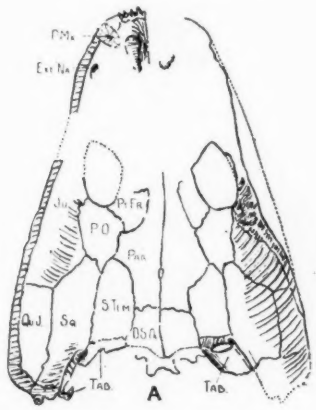

FIG. 54. *Otocratia*. Watson.

OTOCRATIDAE

This family has but a single genus and species and is defined by Watson as follows:

> Anthracosaurs, in which the squamosal has a long suture with the supratemporal and the tabular, the otic notch being very small, placed caudal to the occiput, and entirely surrounded by tabular and squamosal, so that the tympanic membrane was supported by a continuous ring of bone.

Otocratia (fig. 54*A*) was placed in the Anthracosauridae (Smith-Woodward), the Loxommids (Säve-Söderberg), and a distinct family (Watson).

The characters of the family and genus are:

9. Skull with squamosal attached by a long suture with supratemporal and tabular.
10. Orbits small, far forward, widely separated, angulate contour in front.

12. Nares. External nares very small, almost on lateral edge, rather far back. Internal nares (? anterior palatal vacuities) large.
16. Otic notch small, posterior to the occiput and entirely surrounded by the tabular and squamosal; the tympanic membrane was supported by a continuous ring of bone.

This pecular form is so important that the observations of Watson and Säve-Söderberg are quoted. Watson says (1929):

The skull is quite unique in structure, and considering its early date, is of most unexpected character. The table consisting of the dermosupraoccipitals, tabulars, parietals, supratemporals, etc., instead of being sharply marked off from the rest of the skull roof by deeply incised otic notches and by the loose attachment by a moveable articulation, instead of a suture, of the squamosal, is smoothly continuous with and rigidly attached by suture to the cheek. The otic notches are driven downward by a long suture between the tabular horn and a special ridge which rises from the squamosal just above the line at which that bone must have been united with the pterygoid. A special flange which springs from the posterior edge and from the lower surface of the tabular near its admesial border passes downward and outward, below the middle ear until it meets the squamosal at its attachment to the quadrate.

The otic notch is closed behind, as in *Dissorhophus*, *Trematops* and *Cyclotosaurus*, but the completion of the tympanic ring is arrived at in an entirely different manner. The tympanic ring appears to have been a long narrow slit lying on the dorsal surface only just above and in front of the quadrate condyle.

In the close attachment of the table to the rest of the skull and in the closure of the otic notches it is far more advanced than any other Carboniferous Labyrinthodont.

Säve-Söderberg disagreed with Watson and said (1933):

The curious genus *Otocratia*, described by Watson, is probably not nearly related to the *Anthracosauria*. From Watson's figure it seems most probable that this genus has the Loxommoid type of dermal cranial roof, with a parieto-extrascapular (dermosupraoccipital) and small lateral extrascapulars (tabulars). It differs from all Scotch *Anthracosauria*, and agrees with *Cricotus* and with the Ichthyostegids, by having a rather clear postorbito-dermosphenotic (postorbital), meeting the fronto-parietal (parietal). However, in the anterior part of the palate *Otocratia* presents, according to Watson's description, a pronounced similarity to *Pholiderpeton*. And finally it differs both from the *Anthracosauria* and from all Carboniferous Labyrinthodonts, and agrees with the Ichthyostegids, in the very close attachment of the cheeks to the dermal cranial roof. For the present the systematic position of *Otocratia* must be regarded as entirely unknown.

CRICOTIDAE

This family is accepted by all. Watson (1926) gives the following definition of the family: "Anthracosaurs with a narrow, elongated skull, and clavicles of the structure of those found in *Trimerorhachis*." He further remarks:

A separated table described by Case shews that the general structure of the dermal roof of the skull is very much like that of *Eogyrinus*, indeed the table is extraordinarily similar to that of *Pteroplax*. It is clear from the occurrence of several isolated tables that the squamosal was readily disarticulated and a personal examination of the material has shewn me that it had an articulation instead of a sutural attachment.

A fossil which is clearly the basis cranii of *Cricotus*, has been figured although not recognized by Williston (19),[9] it is extremely similar to that of *Paleogyrinus*, possessing large, well formed basipterygoid processes. The occipital condyle is in part exoccipital.

The characters of the family are:

4. Girdles. Clavicles with triangular expansion on the ventral surface, "like *Trimerorhachis*" (Watson).
9. Skull narrow, elongate; squamosal articulated to skull roof-table "very much like *Eogyrinus*"; "extraordinarily similar" to *Paleogyrinus*. Lower jaw "identical" with *Eogyrinus*. (All quotes from Watson.)
10. Orbits large, oval, in the posterior half of the skull.
14. Cornua formed by the tabular, "may" support the pectoral girdle.

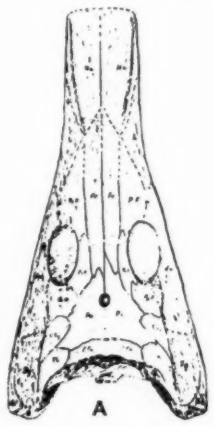

FIG. 55. *Cricotus*. Broom.

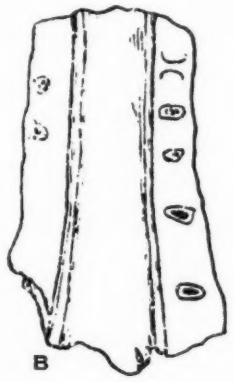

FIG. 56. *Cricotillus*. Case.

Cricotus (fig. 55*A*) is accepted by all. The characters, other than those given for the family, are:

1. Body elongate.
2. Tail elongate.
3. Limbs indicating aquatic life by the breadth of the humerus.

Watson (1926) says:

Cricotus is thus still very incompletely known but appears to differ in little from the Carboniferous *Embolomeri*. It resembles the members of the Anthracosauroideae in all the characters in which that superfamily differs from

[9] The "(19)" given by Watson is meaningless as there is no list of references. He probably refers to figure 10, C.D.E., page 24, of Williston's *Osteology of the Reptilia*. E.C.C.

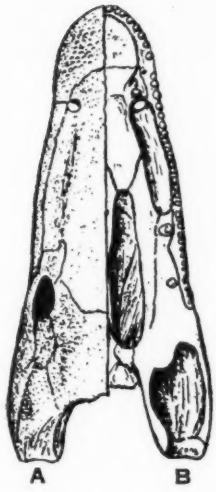

FIG. 57. *Chenoprosopus*. Williston.

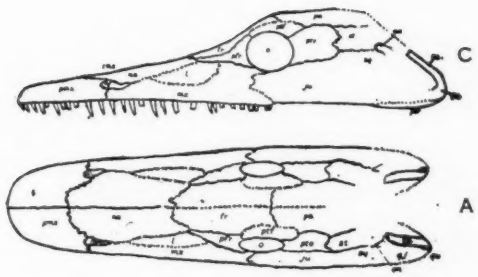

FIG. 58. *Chenoprosopus*. Williston.

the *Loxommodideae*, and must certainly be included in it, forming however a distinct family.

Cricotillus (fig. 56*B*) was named from fragments and is generally placed in the Cricotidae, but is so incompletely known that its position is very uncertain. Williston regarded it as possibly related to *Crossetelos* but there is no proof. Certain intercentra found in the Green Division of the Dunkard, Permian, of West Virginia, and described by J. L. Tilton (1926) are of the *Trimerorhachis* type, but they are so nearly closed into rings that they approximate very closely the *Cricotus* type. Further discovery may show that they belong to a genus of this family.

Chenoprosopus (fig. 57*A*, *B*, 58*A*, *C*) from the Permian of New Mexico. Placed in the Archaegosauridae (Kuhn, Smith-Woodward, Huene), the Cricotidae (Williston, 16), the Eryopidae (Williston, 18), *incertae sedis* (Abel). An incomplete skull. The position of the external nares and the narrow interpterygoid vacuities suggest the Embolomeri, but reference must await further information.

Archeria, from the Wichita, Permian of Texas, may be a Cricotid, as suggested by Romer.

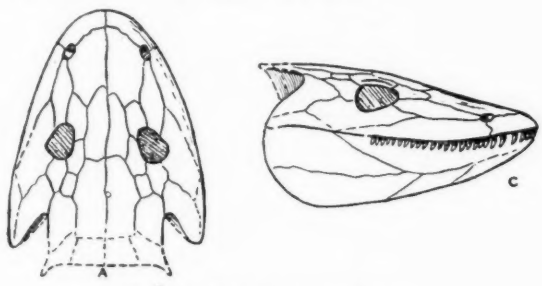

FIG. 59. *Leptophractus*. Romer.

Leptophractus (fig. 59*A*, *C*) has had numerous species referred to it. Certain of these are undoubtedly Cricotids. *L. lancifer* is so regarded (Kuhn, Romer, ? Smith-Woodward), and Watson considered *L. obsoletus* as an *Orthosauriscus* (*Orthosaurus*). Other species have been referred to the Phyllospondyli and the Lepospondyli. *Erpetosaurus* and *Eobaphetes* are regarded as synonyms of *Leptophractus* (Romer, Kuhn). The characters of the genus are:

7. Sculpture of pits and ridges.
9. Skull somewhat elevated; anterior palatal vacuities "improbable"; prevomers large and meet in a large median suture; interpterygoid vacuities "indicating" large size; septomaxillary present. Posterior portion of the skull unknown.
10. Orbits small, slightly triangular; in posterior half of skull.
11. Teeth "extraordinarily" stout and close set, somewhat recurved; dentine infolded in labyrinthine pattern.
12. Nares. External nares small, not terminal. Internal nares large, triangular.
13. Lachrymal extending from orbit to naris.
15. Intertemporal present.
16. Otic notch deep.

Romer (1930) regarded *Eogyrinus*, *Leptophractus*, and *Cricotus* as closely related.

Pholiderpeton (fig. 60*A*) is of uncertain position; it has been put in the Cricotidae (Kuhn, Watson), but the latter remarking on the unsatisfactory condition of the skull, and in a distinct family, Pholidogasteridae (Smith-Woodward). Watson says of the vertebrae (1929):

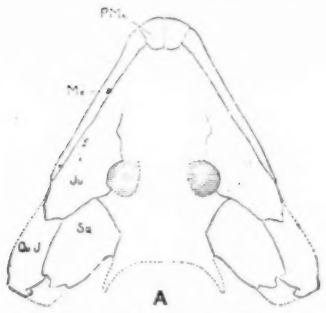

FIG. 60. *Pholiderpeton*. Watson.

Thus these vertebrae present a structure intermediate between that of a typical embolomerous and a rhachitomous vertebrae, resembling the former in the fact that the pleurocentra completely surround the notochord, and the latter in that the intercentra are not complete rings.

This is much like the condition reported by Tilton for the specimens found in the Dunkard, Permian, of West Virginia.

The characters are:[10]

1. Body long, notably the neck; circular in section.
2. Tail long, laterally compressed.
3. Limbs well developed; tarsus (at least) ossified.
4. Girdles well developed. Clavicles "exactly resemble those of *Trimerorhachis* or *Archegosaurus*."
5. Vertebrae of midcaudal region intermediate between rhachitomous and embolomerous.
6. Scutes "a massive plastron of ventral scales."
8. Skull somewhat elongate, nose blunt; palatines reach far forward; interpterygoid vacuities small; pterygoids meet in front (dotted in by Watson); condyle single; squamosal loosely attached to the table of the skull.
10. Orbits elongate oval, widely separated, not lateral.
11. Teeth. Tusks on palatine and a few large teeth on ectopterygoid.
12. Nares. External nares small, oval, widely separated. Internal nares large, elongate, far anterior.

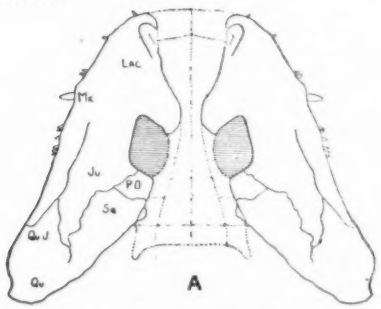

FIG. 61. *Crassigyrinus*. Watson.

[10] The descriptions of *Pholidogaster* and *Pholiderpeton* have been transposed.

14. Cornua formed by tabulars, blunt.
15. Intertemporal present.
16. Otic notch absent.

Crassigyrinus (fig. 61*A*) was put in the Cricotidae (Kuhn, Watson), ? Anthracosauridae (Smith-Woodward). Watson suggested that *Macromerium* (*Macromerion*) may be a synonym but made certain remarks which are reviewed under the description of that genus. The characters are:

9. Skull with wide snout; quadrate region far behind the occiput; maxillary underlies much of the quadratojugal, excluding jugal from orbit.
10. Orbits in midlength of skull, median.
11. Teeth. A large tusk at midlength of the maxillary.
12. Nares. External nares large.

FIG. 62. *Diplovertebron*. Watson.

"*Macromerium*" is of uncertain validity. Lydekker (1889) suggested the name as an emendation of Fritsch's *Macromerion*. Watson (1929) says that it is impossible to refer Lydekker's specimen (*Macromerium*) to Fritsch's genus because the latter was founded on a mixture of material and until a skull of it can be found Lydekker's genus had better be ignored. However, he discusses it under his Anthracosauroideae. Kuhn puts the genus as *Macromerion* under the Cricotidae but says that it is to be discredited ("Die Gattung ist wohl einzuziehen"), Smith-Woodward put it with question in the Cricotidae. Steen (1938) gives a list of Fritsch's species showing how mixed and undependable the material is. It is not possible to give the characters.

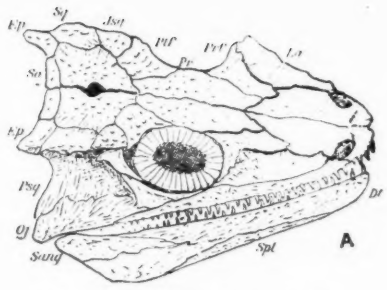

FIG. 63. *Diplovertebron*. Jaekel.

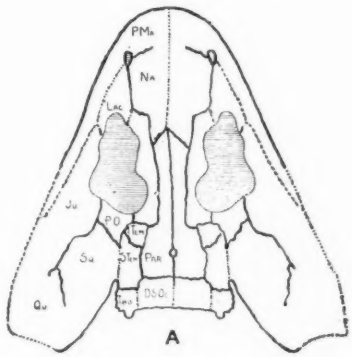

FIG. 64. *Loxomma*. Watson.

Diplovertebron (fig. 62*A*, 63*A*) is generally put in the Cricotidae. Lydekker (1889) suggested the emendation *Diplospondylus* for Fritsch's "hybrid" name. Jaekel's *Gephyrostegus* from the same locality is regarded as a synonym of *Diplovertebron*. The characters are:

1. Body remarkable for its lizard-like proportions.
3. Limbs, Manus with five digits.
4. Girdles. Pubis probably not ossified; girdles as in all advanced amphibians, shoulder girdle indicates terrestrial life.
9. Skull with the palate typically embolomerous.
10. Orbits in midlength of the skull.
12. Nares. External nares far down on the side of the skull.
13. Lachrymal reaches from orbit to naris.
14. Cornua small.
15. Intertemporal present.
16. Otic notch well developed, broad.

LOXOMMOIDEAE

Watson (1929) gives as characters of the superfamily and the family Loxommidae:

9. Prevomers large; maxillary ? excluding jugal from the edge of the skull; squamosal rigidly attached to table of the skull; Steen (1938) adds, large preorbital vacuities confluent with the orbit; narrow postorbital table; very wide nasals.
10. Orbits small, round, but continuous with triangular antorbital vacuities.
11. Teeth. Tusks on palatine and ectopterygoid.
12. Nares. Internal nares small, widely separated.
13. Lachrymal extending from orbit to naris.
14. Cornua absent but a small process on the tabular for muscular attachment.
15. Intertemporal present.

Säve-Söderberg (1935) suggested raising Watson's superfamily to subordinal rank as the Loxommoidei, including *Orthosauriscus* (*Orthosaurus*) and *Macrerpeton*, in addition to Watson's forms, *Loxomma*, *Baphetes*, and *Spathiocephalus*. He said that the Loxommidae are "clearly related to the *Ichthyostegidae*" and are "descendants of primitive representatives of the *Ichthyostegalia*." He added, in the same place, that the two families Loxommidae and Anthracosauridae differ in many important particulars, that they have entirely different phylogenetic positions and that the Loxommidae are a natural link between the Ichthyostegalia and the Permo-Triassic Labyrinthodontia. The Anthracosauridae cannot be derived from the Ichthyostegid-like ancestors and "may even" have arisen from fish independent of the Loxommid line.

Loxomma (fig. 64*A*, 65*A*). Steen (1937) regarded *Sclerocephalus credneri* of Broili as a synonym of *Loxomma* and Watson had the same opinion of *Megacephalus* and *Mioganodon*. The characters are:

9. Skull a little longer than broad, snout rounded; squamosal sutured to the table of the skull.
10. Orbits far back, small, rounded, close together; continuous with a preorbital vacuity.
11. Teeth laterally compressed to form two edges; simply labyrinthine; base tumid; tusks on prevomers, palatines, and ectopterygoids.
13. Lachrymal extending from orbit to naris.

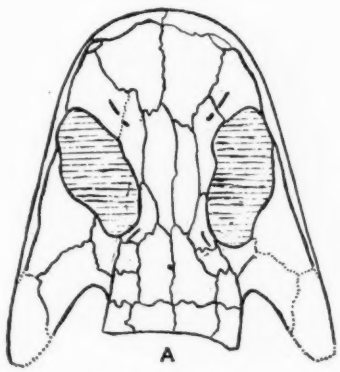

FIG. 65. *Loxomma*. Steen.

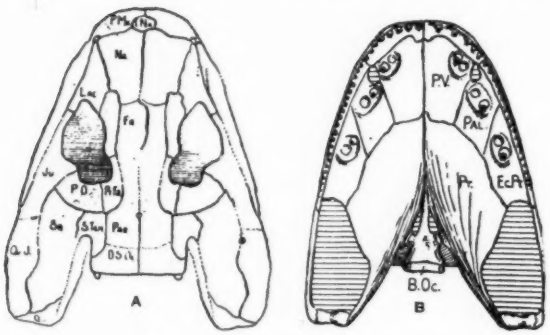

FIG. 66. *Baphetes*. Watson.

14. Cornua absent.
15. Intertemporal present, of "considerable size."

Baphetes (fig. 66*A*, *B*) is accepted by all. Watson gives as the characters of the specimen from Scotland:

9. Basipterygoid process very short and broad, much less clearly marked than in other Embolomeri; septomaxillary present (*B. latirostris*) or absent (*B. planiceps*); anterior palatine vacuities absent; maxillary does not underlie quadratojugal; a small internasal present.
10. Orbits elongate.
11. Teeth. Ten in each premaxillary; a single row on maxillary; tusks on prevomer, palatine, and ectopterygoid.
12. Nares. External nares extraordinarily small, "very near ventro-lateral margin of snout" (Säve-Söderberg 1932).
13. Lachrymal extending from orbit to naris.
15. Intertemporal absent.

Baphetes planiceps from Pictou, Nova Scotia, has the following characters according to Moodie:

9. Skull large, broader than long.
10. Orbits well forward.
11. Teeth large, heterodont, a single row.

Other specimens from South Joggins and Pictou, Nova Scotia, were regarded as indeterminate by Steen and Romer.

Orthosauriscus (fig. 67*A*, *B*, *C*), for *Orthosaurus* preoccupied. *Megacephalus* of Barkas is a synonym of *Orthosauriscus*. The genus is put by all in the Loxommidae. The characters are:

9. Skull high posteriorly; condyle single, deeply cancave; septomaxillary present; supraoccipital present, small; parasphenoid and basisphenoid present, distinct; basisphenoid movably articulated to pterygoid; interpterygoid vacuities small or absent; anterior palatal vacuities large, perhaps penetrating the roof; internasal present; articulation for lower jaw well behind posterior edge of skull.
10. Orbits very large, elongate or small, round and continuous with triangular preorbital vacuities.
11. Teeth. Tusks on palatine in a single row.
12. Nares. External nares small, lateral, very near ventro-lateral margin of snout (Säve-Söderberg 1932). Internal nares elongate, oval, near sides.
13. Lachrymal not reaching naris.
14. Cornua limited to a small rugosity probably for attachment of posttemporal.
16. Otic notch obvious.

Steen (1931) cites a fragment of a cheek from the Pennsylvanian of Linton, Ohio, which she says "can not be distinguished from the English specimens of *Orthosaurus*."

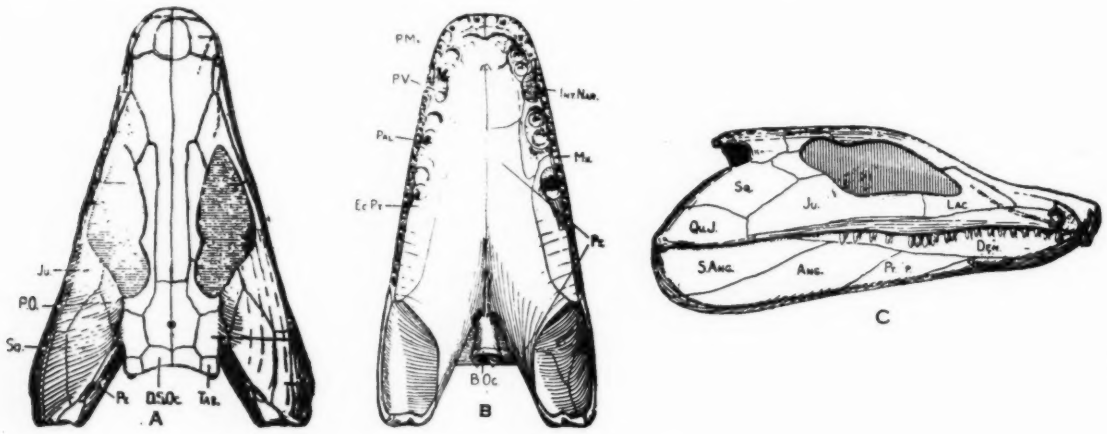

FIG. 67. *Orthosauriscus*. Watson.

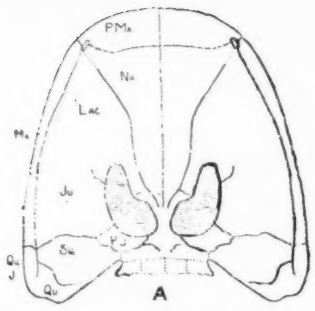

FIG. 68. *Spathiocephalus*. Watson.

Spathiocephalus (fig. 68*A*) is placed by all in the Loxommidae. The characters are:

9. Skull broad as long, nearly square; postorbital region very short, and bones short and wide; parietal, frontal and prefrontal fused in the narrow interorbital bar; facial region very long; process of parasphenoid with rugose ridges, no trace of fenestra ovalis; parasphenoid-basisphenoid movably articulated with the pterygoid; interpterygoid vacuities small; pterygoids united anteriorly; pineal foramen absent; articulation for lower jaw posterior to the condyle.
10. Orbits near median line, far back, kidney-shaped, joined to preorbital vacuities.
11. Teeth with base fluted, slightly expanded, tips blunt and turned back in a chisel edge (as in *Cricotus*).
12. Nares. External nares very small, widely separated, nearly terminal.
13. Lachrymal "appears" to reach nares.
14. Cornua formed by tabular, small.
16. Otic notch deep.

DENDRERPETONTIDAE

Perhaps this is the Cricotidae of Watson. Family characters are those of the genus.

Dendrerpeton (*Dendrerpetum* of Lydekker) (fig. 69*A*, *B*, *C*) is one of the sadly confused genera. It has been referred to the Branchiosauridae (Kuhn), Hylonomidae (Smith-Woodward), Anthracosauridae (Moodie), Embolomeri (Steen). Fritsch proposed the family Dendrerpetontidae (emended to Dendrerpetidae by Lydekker) to include Owen's *Dendrerpeton* from Nova Scotia and certain doubtful specimens from Bohemia, as opposed to the Microsauria. Lydekker included certain Brachyopids which certainly do not belong with *Dendrerpeton*. The specimen from Linton, Ohio (*D. obtusum*), belongs in some other genus, *Pelion*, *Erpetosaurus*, or *Tuditanus*. According to Steen (1934) the specimens called *Dendrerpeton* from Bohemia either belong in other genera or are indeterminate. The single satisfactorally known specimen of the genus, and probably of the family, is the *D. acadianum* from Nova Scotia. Its characters are:

1. Body generally lizard-like.
2. Vertebrae intermediate between rhachitomous and embolomerous (Steen 1934), as in *Pholidogaster*.
9. Skull high; occipital condyle single, deeply cancave, parasphenoid movably articulated to the pterygoid; interpterygoid vacuities small; pterygoids do not meet in middle line.
10. Orbits in midlength of skull, widely separated.
11. Teeth. Tusks on palatine and ectopterygoid; denticles on parasphenoid.
12. Nares. External nares small, widely separated.
14. Cornua dependent, form a notch visible from the side.

Steen (1934) lists the following points to show the intermediate position of *D. acadianum* between the Rhachitomi and Embolomeri.

1. Skull high (Embolomeri).
2. Basipterygoid process of the parasphenoid movably articulated with the pterygoid. (Embolomeri and in some Rhachitomi; not in the later Rhachitomi.)
3. Pterygoids do not meet in the midline in front (Embolomeri).
4. Single occipital condyle (Embolomeri and early Rhachitomi).
5. Flanges of the dermosupraoccipital and tabular extend into the occiput (Rhachitomi).
6. Supraoccipital ossified (Embolomeri and some Rhachitomi, as *Eryops*), unossified in most Rhachitomi and all Stereospondyli.

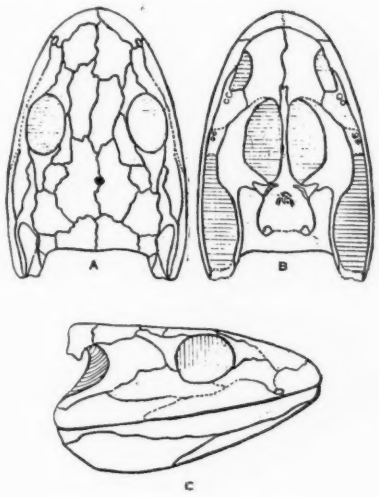

FIG. 69. *Dendrerpeton*. Steen.

The following genera have been placed in the Embolomeri but are either indeterminate or *incertae sedis*.

Arkanserpeton from the Allegheny Formation, Pennsylvanian, of Arkansas. A single femur, indeterminate.

Capetus from the Westphalian of Nyran. An incomplete posterior half of a skull. Labyrinthodontia *incertae sedis*.

Eosaurus from the Carboniferous of South Joggins, Nova Scotia. Two vertebrae which have been variously referred, the present inclination seems to be to place them in the Embolomeri.

Gaudryia from the Westphalian of Nyran, Bohemia. The anterior half of a palate and lower jaws. Placed in the Melosauridae (Kuhn), the Cochleosauridae (Smith-Woodward), and as an indeterminate Embolomere (Steen 1938).

Ichthyerpeton from the Jarrow Colliery, Carboniferous, of Kilkenny, Ireland. Impression of the elongate, *Amphiuma*-like body, with weak posterior limbs. Placed in the Amphiumidae (Kuhn), Nyranidae (Moodie), Embolomeri (Smith-Woodward). Moodie's *Ichthyerpeton squamosum* was regarded by Romer (1930) as a synonym of *Ophiderpeton*. It is indeterminate.

Nummulosaurus from the Westphalian of Tremosna. A mixture of ribs, vertebrae and scales. It was placed in the Embolomeri (Kuhn), Orthosauridae (Smith-Woodward), and as indeterminate (Steen).

Papposaurus from Scotland. A single femur. Placed in the Reptilia (Watson), the Stegocephalia questionably (Kuhn), but he also lists it in his catalog of the Cotylosauria. The bone has the characters of certain Embolomeri, notably in the adductor ridge which is straight, not oblique.

Spondylerpeton from the Allegheny Formation, vertebrae which are embolomerous, but otherwise indeterminate.

RHACHITOMI

The approach to a consensus of opinion as to the structure and classification of the Rhachitomi and the Stereospondyli is far greater than in the Phyllospondyli and the Lepospondyli. This is in large part owing to the better preservation of the material, a fact which is evidenced by the discovery, especially by Steen, that a considerable number of specimens previously referred to the Phyllospondyli and the Lepospondyli are associated with vertebrae of the rhachitomous type. The occurrence of similar adaptive modifications in the different groups has been the cause of most of the erroneous identifications and references.

There have been eighteen families suggested for the Rhachitomi:

Acanthostomidae
Achelomidae
Actinodontidae
Archegosauridae
Benthosuchidae (Benthosauridae)
Cochleosauridae
Dissorophidae
Dwinasauridae
Eryopidae
Lydekkerinidae
Melosauridae
Micropholidae
Nyranidae
Platyopidae
Rhinesuchidae (Rhinosauridae)
Trematopsidae
Trimerorhachidae
Zatrachydae

Several of these must be dropped because of synonymy, preoccupation, or other error; those retained are described below with their constituent genera.

List Showing the Classification, Geological Horizon, and Location of the Determinable Rhachitomi

Acanthostomidae
Acanthostoma, Middle Rothliegende, Plauenschengrund, near Dresden, Germany.
Achelomidae
Acheloma, Lower Permian, Clear Fork, Texas, U.S.A.
? *Sclerothorax*, Middle Triassic, Middle Bunter, Upper Hesse, Germany.
Actinodontidae
Actinodon, Lower Permian, Autunien, Central France. ? Permo-Carboniferous of Kashmir, India.
Archegosauridae
Archegosaurus, Lower Permian, Saarbrucken, Germany. Lower Permian, Rothliegende, Moravia. ? Lower Permian, Kashmir, India.
Benthosuchidae
Benthosuchus, Upper Permian, North Dwina River, Russia. Eotriassic, Sharsanga River, Russia.
Volgasuchus, Eotriassic, Upper Volga River, Russia.
Cochleosauridae
Cochleosaurus, Lower Carboniferous, Westphalian, of Nyran, Czechoslovakia.
Dissorophidae
Zygosaurus, Middle Permian, of Orenburg Region, South Russia.
Dissorophus, Lower Permian, Clear Fork, of Texas, U.S.A.
Cacops, Lower Permian, Clear Fork, of Texas, U.S.A.
Aspidosaurus, Lower Permian, Clear Fork, of Texas, U.S.A.
Alegeinosaurus, Lower Permian, Clear Fork, of Texas, U.S.A.

XUM

Broiliellus, Lower Permian, Clear Fork, of Texas, U.S.A.

Dwinasauridae

Dwinasaurus, Upper Permian, Tatarian, of North Dwina River, Russia.

Eryopidae

Eryops, Lower Permian, Wichita and Clear Fork, of Texas, U.S.A.

Edops, Upper Stephanian, Moran and Pueblo Formations, of Texas, U.S.A.

Lydekkerinidae

Lydekkerina, Middle Triassic, Middle Beaufort, of the O.F.S., South Africa.

Putterillia, Middle Triassic, Middle Beaufort, of the O.F.S., South Africa.

Melosauridae

? *Melosaurus*, Permian, Orenburg, Russia.

Micropholidae

Micropholis, Lower Middle Triassic, Middle Beaufort, Cape Province, South Africa.

Nyranidae

Nyrania, Westphalian, of Nyran, Czechoslovakia.

Platyopidae

Platyops, Upper Kungurian, Cupriferous sandstone, of Orenburg Region, Russia.

Rhinesuchidae

Rhinesuchus, Lower Middle Triassic, Lower Middle Beaufort, of Nyassaland, South Africa. Permian of Rhenish Prussia. Permian of Madagascar.

Rhinesuchoides, Permian, Tapinocephalus zone, of Cape Province, South Africa.

? *Gondwanasaurus*, Stephanian, Bijori Group, of Bijori, India.

Laccosaurus, Lower Middle Triassic, Lower Beaufort, of Cape Province, South Africa.

Laccocephalus, Upper Permian or Lower Triassic, of O.F.S., South Africa.

Uranocentrodon, Lower Triassic, of Senekal, O.F.S., South Africa.

Trematopsidae

Trematops, Lower Permian, Clear Fork, of Texas, U.S.A.

Trimerorhachidae

Trimerorhachis, Lower Permian, Wichita and Clear Fork, Texas, U.S.A.

Tersomius, Lower Permian, horizon uncertain, Texas, U.S.A.

Zatrachydae

Zatrachys, Lower Permian, Wichita, of Texas, U.S.A.

Platyhistrix, Lower Permian, of New Mexico, U.S.A.

Dasyceps, Lower Permian, of Kenilworth, Warwickshire, England.

Stegops, Middle Carboniferous, Allegheny Formation, Linton, Ohio, U.S.A.

Platyrhinops, Middle Carboniferous, Allegheny Formation, Linton, Ohio, U.S.A.

ACANTHOSTOMIDAE

This family with its single genus was long considered as belonging in the Phyllospondyli but the discovery by Steen (1937) that the vertebrae were of the rhachitomous type necessitated its transference to the Rhachitomi.

Acanthostoma (fig. 70*A*, *B*, *C*, 71*A*, *B*) is accepted by all. The characters of the family and genus are:

5. Vertebrae. "The vertebrae are, however, Labyrinthodontian type, although unique in the structure of the centra (both pleura- and intercentra being ossified as right and left hemicylinders unfused in the mid-dorsal or mid-ventral line)" (Steen 1937).
9. Skull broad and flat; internasal opening prominent between external nares but no bone in the opening; quadratojugal has three spines on ventral margin; antorbital region depressed into a pit as in *Zatrachys;* a single anterior palatal vacuity between prevomers and premaxillaries; interpterygoid vacuities moderate; parasphenoid movably articulated with pterygoid. Prevomer large. Lower jaw has five projections on the angular; dentary long, slender.

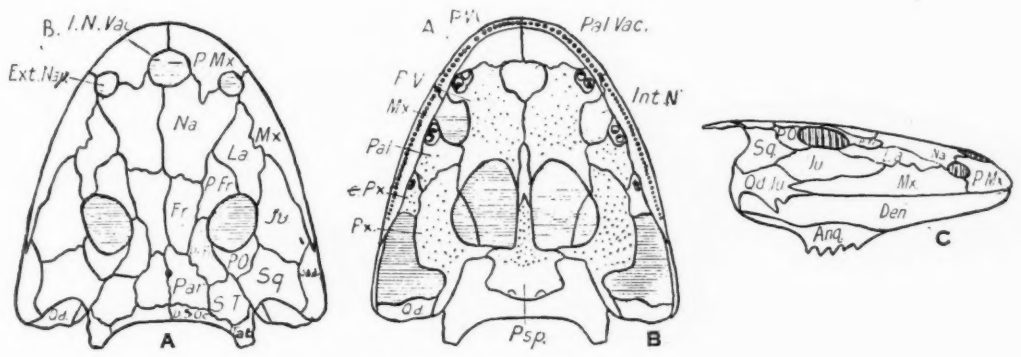

FIG. 70. *Acanthostoma*. Steen.

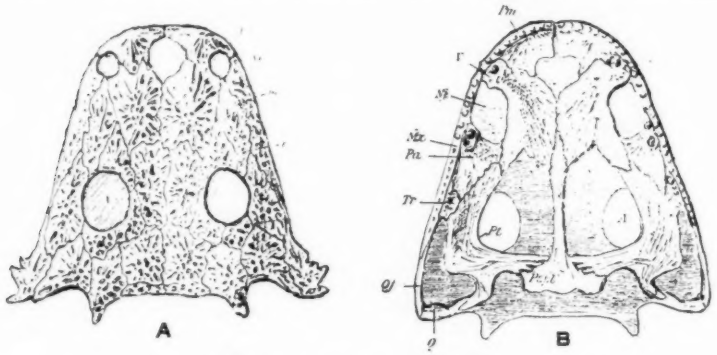

FIG. 71. *Acanthostoma*. Jaekel.

10. Orbits small, widely separated, in posterior half of skull.
11. Teeth. Tusks on palatines, prevomers and ectopterygoid; denticles on all palatal bones.
12. Nares. External nares medium size, lateral. Internal nares large, lateral.
13. Lachrymal extends from orbit to naris (Jaekel), or nearly to naris (Steen).
14. Cornua formed by tabular, short.
15. Intertemporal absent.
16. Otic notch not deep.

Because of the projections on the quadratojugal and the angular, the preorbital pit and the internasal opening, there has been suggested a relationship to *Zatrachys*.

ACHELOMIDAE

This family has but a single genus.

Acheloma is placed in this family, though tentative suggestions (Williston, Smith-Woodward, Romer) have been made that it may be synonymous with or closely related to *Trematops*. Watson (1919) declared that "it has no known allies."[11]

No attempt has been made at an analysis or restoration of the skull as the sutures cannot be made out, but from such descriptions and figures as have been given the characters of the family and genus are:

1. Body relatively short and stout.
3. Limbs. Anterior limbs short, well developed.
4. Girdles. Thoracic girdle strong.
9. Skull high, snout narrow; interpterygoid vacuities large.
10. Orbits large, midlength of the skull; looking laterally and upward.
11. Teeth subequal, larger anteriorly; tusks on palatine.
14. Cornua absent.
16. Otic notch absent, "obliterated" according to Watson (1919).

[11] But see the excellent figures and descriptions of *Acheloma* and *Trematops* by Olson, *Jour. Geol.* **49** (2), 1941.

ACTINODONTIDAE

A family proposed by Watson to include *Actinodon* and its synonyms, which are all usually included in the Eryopidae. The confusion is illustrated by Watson placing *Weissia* in the Actinodontidae because it is a synonym of *Sclerocephalus*, which other workers place in the Eryopidae.

Watson distinguished the two families, Actinodontidae and Eryopidae, as follows:

1. Orbits in the midlength of the skull in *Actinodon* instead of in the posterior half as in *Eryops*.
2. The proximal ends of the clavicles expanded in *Actinodon*, not so much in *Eryops*.

Thevenin described the prevomers of *Actinodon* as larger than in *Eryops* and covered with denticles, but Sawin (1941) shows clearly a large prevomer in *Eryops* and says, "Tiny denticles, not apparent in the figure, are to be found over much of the palatal surface except on the parasphenoid." It is obvious that such differences may be due to age or to differences less than familial or generic. The distinction between the two families is questionable, they are possibly geographical varieties.

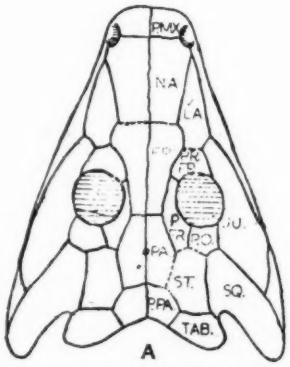

FIG. 72. *Actinodon*. Westoll.

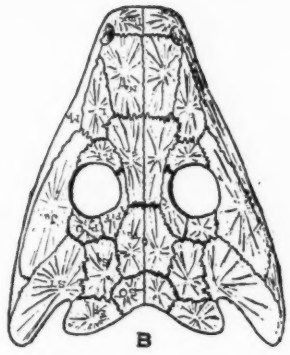

FIG. 73. *Actinodon*. Lydekker.

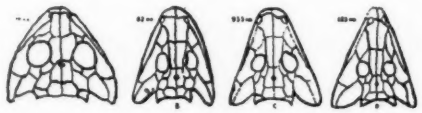

FIG. 74. *Actinodon*. Showing growth stages, Romer.

Actinodon (fig. 72*A*, 73*B*, 74) has been placed in the Actinodontidae (Kuhn, Watson) and the Eryopidae (Smith-Woodward and others). *Euchirosaurus*, *Chelydosaurus* (*Chelyderpeton*), *Weissia*, and ? *Osteophorus* are generally regarded as synonyms.

The characters of the family and genus are:

1. Body heavy, stout.
2. Tail short.
3. Limbs strong; carpus and tarsus well ossified.
4. Girdles strong; bones of the pelvis coössified; proximal ends of clavicles expanded.
8. Scutes more or less hexagonal, a close mosaic distinct from the awl-like gastralia.
9. Skull moderately depressed; occipital condyle triple; a distinct basipterygoid process articulating movably with the pterygoid; interpterygoid vacuities medium size; a notable change in form by proportional elongation of the skull with age.
10. Orbits small, in midlength of the skull.
11. Teeth with infolded dentine, hardly labyrinthine.
12. Nares. External nares nearly terminal.
13. Lachrymal touches neither orbit nor naris.
14. Cornua short, stout, formed by tabular.
15. Intertemporal absent.
16. Otic notch small but distinct.

Sclerothorax (fig. 75*A*, *B*) was placed in the Actinodontidae (Huene, Kuhn) despite its broad snout and high geological position. The characters given by Huene are:

9. Skull broad, little longer than wide, snout blunt; depressed between orbits; supratemporal region higher; parasphenoid short and broad, sutured to pterygoid; anterior palatal vacuities absent; anterior ends of the pterygoids widely separated, do not touch prevomers; sensory grooves absent; postorbital peculiar in extending laterally from orbit as in *Cyclotosaurus* and *Capitosaurus*.
10. Orbits small, separated, in midlength of the skull.
11. Teeth. Large teeth on prevomers and palatines; a palatal row paralleling the maxillary row, mostly isodont.
12. Nares. External nares small, round, nearer the midline than lateral, not terminal. Internal nares small, near midline of skull.
13. Lachrymal touches neither orbit nor naris.
14. Tabular ? present, the posterior portion of the skull imperfect.
16. Otic notch deep.

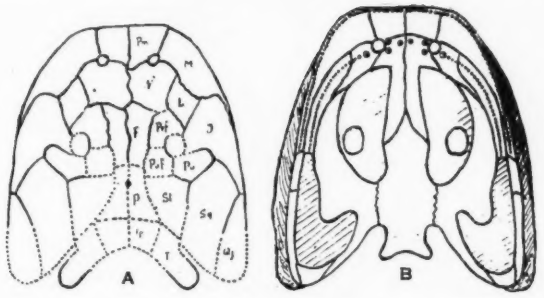

FIG. 75. *Sclerothorax*. Huene.

It is evident that Huene lists many characters that suggest the Stereospondyli.

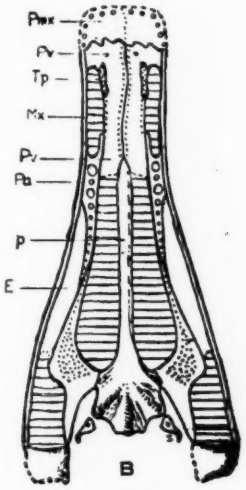

FIG. 76. *Archegosaurus*. Whittard.

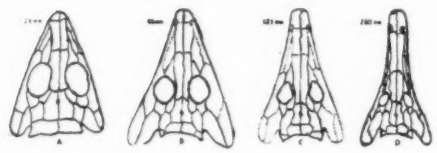

FIG. 77. *Archegosaurus*. Showing growth stages, Romer.

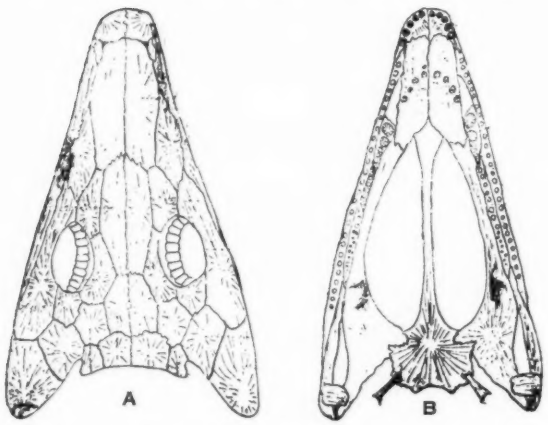

FIG. 78. *Archegosaurus*. Hofker.

ARCHEGOSAURIDAE

The abundance of material has permitted recognition of growth stages and notable changes of form with increasing age. Various stages or imperfect specimens have been referred to other genera, as *Sparagmites* and its synonym *Chalcosaurus* (*Chalcochelys* by *lapsus*), *Discosauriscus* (for *Discosaurus* preoccupied), and *Melosaurus*. The fish *Pygopterus* was originally referred to *Archegosaurus* by Agassiz.

Archegosaurus (fig. 76*B*, 77 showing stages of growth, 78*A*, *B*) is accepted by all. The characters of the family and genus are:

1. Body elongate.
2. Tail elongate, ? vertically expanded.
4. Girdles. Thoracic girdle with well developed clavicles and interclavicle.
7. Sculpture of pits and radiating ridges.
8. Scutes on venter.
9. Skull much elongate in the adult; occipital condyle triple (Watson), triple or double (Smith-Woodward), ossified only in old individuals; parasphenoid and basisphenoid sutured to the pterygoid; pterygoids extend forward to prevomers; interpterygoid vacuities large; no anterior palatal vacuities.
10. Orbits small, far back in the adult.
11. Teeth. Tusks on palatines and prevomers; a palatal row paralleling the maxillary row.

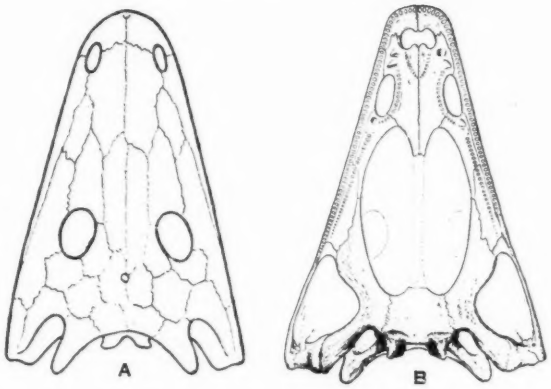

FIG. 79. *Benthosuchus*. Bystrow and Efremov.

12. Nares. External nares oval, lateral. Internal nares elongate, lateral.
13. Lachrymal touching neither orbit nor naris.
14. Cornua slight or absent.
15. Intertemporal absent.
16. Otic notch small.

BENTHOSUCHIDAE (BENTHOSAURIDAE)

This family includes *Benthosuchus* (for *Benthosaurus* preoccupied) and *Volgasuchus* of Efremov; together with *Wetlugasaurus* they constitute his group of Neorhachitomi which forms the connecting link

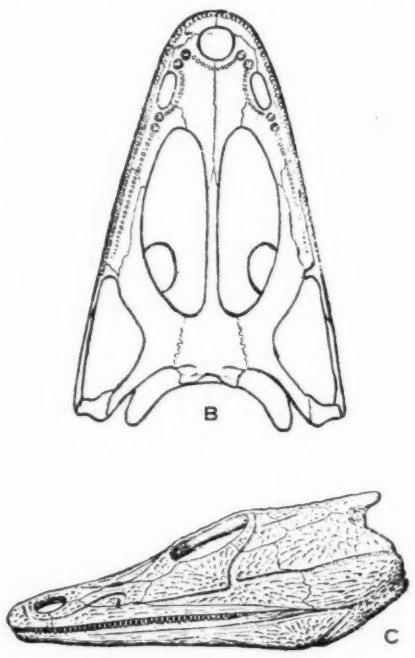

FIG. 80. *Benthosuchus*. Bystrow and Efremov.

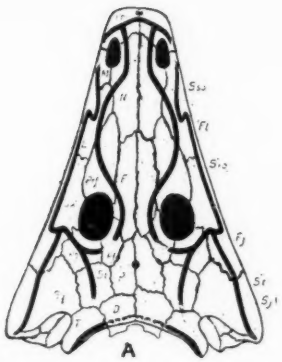

FIG. 81. *Benthosuchus*. Bystrow

between the Rhachitomi and the Stereospondyli. The characters of the family are those of the genera.

Benthosuchus (fig. 79*A*, *B*, 80*B*, *C*, 81*A*, 82*A*) (for *Benthosaurus* preoccupied) was placed in the Trematosauridae (Kuhn), Rhinesuchidae (Smith-Woodward), Benthosuchidae (Säve-Söderberg). Bystrow and Efremov (1940) gave a detailed account of the changes in the skull with age. This is so illustrative of what we might expect to find in other forms, if as complete material were at hand, that their statement is reviewed somewhat *in extenso*.

The remains of *Benthosuchus* and the nearly related *Wetlugasaurus* were found in enormous numbers in the Eotriassic deposits of Russia, which occur over a large area in the northeastern part of the Russian basin. The formation is exposed more or less connectedly from the forty-eighth to the fiftieth degrees of east longitude, and from the fifty-sixth to the sixty-sixth degree of north latitude. Within this area the bones of *Benthosuchus* were found almost without any intermixture of the bones of other forms in the northern, geologically older, gray sandstone of the Scharsanga River. A similar deposit, composed almost exclusively of the bones of *Wetlugasaurus*, was found in a southern, geologically younger, exposure of the gray sandstone in the Wetluga River district. These two districts yielded a large amount of material. Efremov collected over fifteen hundred specimens of *Benthosuchus* in excavations not exceeding two hundred square meters and calculated that in the whole area of the Eotriassic there must be "hundreds of thousands" of individual bones.

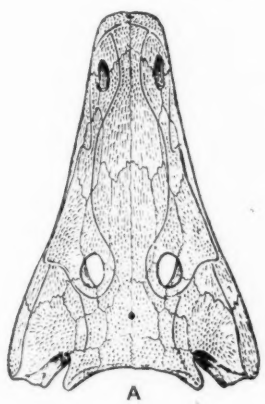

FIG. 82. *Benthosuchus*. Bystrow and Efremov.

The wealth of material uncovered, the almost complete restriction of the material to a single genus and species in each of the two areas, warrant Bystrow and Efremov in the conclusions they have drawn.

Confining their discussion almost entirely to the genus *Benthosuchus*, the authors show that they have individuals ranging in size from skulls 27.5 mm. long to 700–800 mm. long. These intergrade so closely that any separation by size is impossible. It is notable that in all the wealth of material of forms certainly aquatic in habit there is no occurrence of material that suggests a larval stage, or a stage of metamorphosis. The changes are those of growth after the adult form of body was established. Even if the material was accumulated by flood water sweeping over large areas, as suggested by the authors, it is hardly possible that all traces of a larval condition would have been destroyed. If we accept, as we are justified in doing, the premises and conclusions of the authors, we have in their summary a very strong argument for questioning the value of both size and contour of the bones of the skull as criteria for the determination of genera and species. This was the opinion expressed by Steen in 1937.

The authors give the following list of characters marking the difference between the young, adult, and aged (as determined by size) of *Benthosuchus sushkini*.

Characters of young *Benthosuchus:*

1. Skull short, triangular; snout round, wide; lateral margins straight.
2. Orbits very large, in middle of skull.
3. External nares widely separated, terminal.
4. Pineal foramen in line with the posterior edges of the orbits.
5. Preorbital and postorbital elements of the roof of almost the same size; of considerable width.
6. Skull high in the occipital region, transversely arched, edges comparatively flat.
7. Slight bend of interorbital region.
8. Strong curve in sulcus supraorbitalis.
9. Cornua short; otic notch shallow, wide.
10. Body of the parasphenoid very wide.
11. Process of the parasphenoid short, wide.
12. Processus vomeris of the parasphenoid wide.
13. Anterior ramus of the pterygoid comparatively short, equal in length to the posterior ramus.
14. Fenestra premaxillaris single, traces of cartilage in the space.

15. Foramen nervi vagi comparatively large.
16. Fenestra supraoccipitalis large, high.
17. Fenestra basioccipitalis low, wide.
18. Processus submedullaris and processus lamellosus exoccipitalis undeveloped.
19. Lamina parapterygoidea squamosi high as compared with low ramus postpterygoidea; between the two above bones a slit.
20. Crista obliqua pterygoidea undeveloped.
21. Osseus tuberculum on posterior face of the quadrate absent.

Characters of the middle aged and adult *Benthosuchus:*

1. Skull elongate, narrow, strongly widened in posterior region; snout narrow; lateral margin concave.
2. Orbits small, more posterior than in the young.
3. External and internal nares close together; external nares oval, not terminal.
4. Pineal foramen posterior to the posterior edges of the orbits.
5. Preorbital elements of the roof strongly developed, elongate; the postorbital elements less developed, more nearly square.
6. Occipital region low; arch of cranial roof concave; lateral margins concave; the arching due to downbending of the lateral parts.
7. A strong down bend of the antorbital region.
8. Slight curvature of the sulcus supraorbitalis.
9. Otic notch deep, narrow; cornua elongate.
10. Body of the parasphenoid a longitudinally elongate parallelogram.
11. Process of parasphenoid long, narrow.
12. Processus vomeris of parasphenoid long, narrow.
13. Anterior ramus of the pterygoid comparatively elongate, averaging 1½ times the posterior ramus.
14. Fenestra premaxillaris divided by an incomplete septum; in old age undoubtedly an ossified septum making the opening double.
15. Foramen nervi vagi relatively small.
16. Fenestra supraoccipitalis wide, low; reduced by downward extension of the dermosupraoccipital.
17. Fenestra basioccipitalis small, narrow.
18. Processus submedullaris and processur lamellosus strongly developed.
19. Lamina parapterygoidea low, somewhat less in height than posterior ramus of pterygoid. The slit disappears.
20. Crista obliqua pterygoidea well developed.
21. Strong tubercle on posterior side of quadrate.

To these progressive changes with age the authors list the following individual variations shown in the numerous specimens.

1. In the outline of the sutures; i.e., in the "exposures" of the individual bones noted by Steen.
2. In the general shape of the skull.
3. In the relative size of the openings, external and internal nares, orbits, otic notch.
4. The course of the lateral line system was found to vary in only one skull.
5. In the position of the rows of teeth on the vomers.
6. In the massiveness of the occipital elements.
7. In the position and size of the outlet of the glossopharyngeal nerve.
8. In the size and position of the area covered by denticles on the parasphenoid bone.

It is emphasized by Bystrow and Efremov that definitive peculiarities are developed with age; young specimens of *Wetlugasaurus*, the nearest relative of *Benthosuchus*, are distinguished with far greater difficulty than adult specimens; in the young the resemblance reaches an "extreme degree." The greatest age changes amount to what would be considered as generic differences if a complete series were not at hand. Extreme individual variations would be considered as specific differences.

Using the numbers employed throughout this paper, the characters of young and old specimens are (Bystrow and Efremov 1940):

Young specimens:

9. Skull comparatively short, triangular, snout round, sides straight, occiput high; process of the parasphenoid wide, short.
10. Orbits large, in midlength of skull.
12. Nares. External nares widely separated, terminal. Internal nares oval, widely separated.
14. Cornua short.
15. Intertemporal absent.
16. Otic notch short, wide.

Old specimens:

9. Skull elongate, snout narrow; posterior portion of the skull strongly widened, sides concave; occiput low; process of the parasphenoid long and narrow; anterior palatal vacuity single, parasphenoid sutured to the pterygoid.
10. Orbits small, in posterior half of the skull.
12. Nares. External nares oval, not terminal. Internal nares close together.
13. Lachrymal touches neither orbit nor naris.
14. Cornua formed by the tabular, elongate.
15. Intertemporal absent.
16. Otic notch deep and narrow.

Bystrow and Efremov (1940) make the following propositions concerning *Benthosuchus.*

The high degree of chondrification, "not inferior" to that of the Triassic Stereospondyli, indicates an aquatic mode of life.

XUM

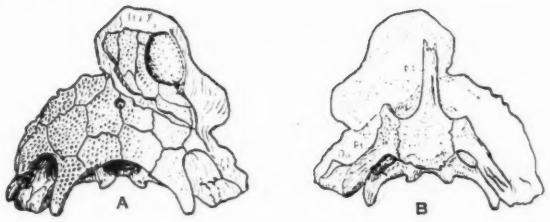

FIG. 83. *Volgasuchus*. Efremov.

That *Benthosuchus*, *Capitosaurus*, *Wetlugasaurus*, and probably *Mastodonsaurus* belong in one group.

That *Benthosuchus* is more primitive than *Capitosaurus* in the long process of the pterygoid and the posterior position of the articulation for the lower jaw.

That the resemblance of *Benthosuchus* to *Trematosaurus* is due to convergence.

That *Benthosuchus* is most closely related to *Rhinesuchus* among the Rhachitomi.

Volgasuchus (fig. 83*A*, *B*) has the characters:

9. Skull. Sensory canals absent; posterior portion of the parasphenoid rectangular, the process rather massive; parasphenoid sutured to the pterygoid.
10. Orbits oval, separated, near midlength of the skull; smaller than in *Wetlugasaurus*.
14. Cornua formed by tabular, elongate.
16. Otic notch long.

Efremov says that *Volgasuchus* is a specialized form of *Wetlugasaurus* not yet fully characterized. Both this and the preceding genus are notable for a precocious stage of chondrification such as occurs in the Phyllospondyli.

In 1929 Efremov used the term "progressive rhachitomi" in calling attention to the condition of the vertebrae of certain early Triassic Stegocephalians, intermediate between the true rhachitomous type and the stereospondylous type. Notable among these is *Benthosuchus*. Huene in 1932 noted the same thing in *Sclerothorax* and said the same could be found in Lydekker's *Laccosaurus*, *Laccocephalus*, and *Micropholis*. Bystrow and Efremov, and later Efremov in 1940, went more into detail, using the term Neorhachitomi, and including in this group *Benthosuchus* and the form *Wetlugasaurus*, usually placed with the Stereospondyli. In their joint paper Bystrow and Efremov discussed *Benthosuchus* and *Wetlugasaurus* as typical Neorhachitomi and mention as belonging to the group *Sclerothorax*, *Dwinasaurus*, and *Platyceps*, but did not include the South African forms mentioned by Huene. In all these forms the anterior vertebrae (cervicals?) approach the sterospondylous type by the loss of the pleurocentra, or their fusion with the hypocentrum or neurocentrum.

The transition took place largely in the early Triassic but not exclusively, as there were Neorhachitomi in the Upper Permian (*Dwinasaurus*) and some Rhachitomi persisted well into the Triassic (certain of the Rhinesuchidae). The transition took place, according to Bystrow and Efremov (1940), in four ways:

1. Complete and simultaneous fusion of the hypocentrum, neurocentrum, and the pleurocentra; e.g., *Dwinasaurus*.
2. Fusion of the pleurocentra first with the neurocentrum and later with the hypocentrum; e.g., *Platyops*.
3. Fusion of the hypocentrum with neurocentrum and later with the pleurocentra; e.g., *Micropholis*.
4. Reduction of the pleurocentra to final disappearance and widening of the upper ends of the hypocentrum and fusion with neurocentrum; e.g., *Benthosuchus* and *Wetlugasaurus*.

The word "fusion" used in the English summary furnished by Russian authors must, obviously, be meant to convey the idea of close association in some instances, as in the relation of the hypocentrum to the neurocentrum. The transition from one type of vertebra to another is regarded by all who have discussed it as one of the deep-seated trends in the evolution of the Stegocephalia and has been accomplished in various ways.

Bystrow and Efremov (1940) reached certain conclusions:

1. The Rhachitomi have a various "make up" of the vertebrae.
2. There are minor methods in the development of the Stereospondyli.
3. The stereospondylous vertebrae produced by fusion [*sic*] of the neurocentrum and hypocentrum are not all notochordal in the strict sense.
4. True notochordal vertebrae are produced by passing through the neorhachitomous stage by complete loss of the pleurocentra.

It is very possible that most of the methods of transition listed by Bystrow and Efremov were abortive and did not continue to the production of true stereospondylous forms. The only method that can be followed with any certainty is the fourth; i.e., development and close articulation of the neurocentrum and hypocentrum and the complete loss of the pleurocentra. This line includes, according to Bystrow and Efremov (1940), *Benthosuchus*, rhachitomous, of the Upper Permian, *Benthosuchus* and *Wetlugasaurus*, neorhachitomous, of the Eotriassic, *Capitosaurus* (or Capitosauridae), stereospondylous, of the middle and upper Triassic. In suggesting and defending this series Bystrow and Efremov make certain their position on several points in opposition to Säve-Söderberg.

They maintain that Säve-Söderberg's reference of *Benthosuchus* to *Mastodonsaurus* is an error because the concave lateral margins of the skull in *Benthosuchus*, emphasized by him, are not present in the young specimens, and further, that his idea of the skull of *Mastodonsaurus* was obtained from the picture by Fraas in which the concavity of the lateral margins is due to the crushing of the specimens and was not corrected in the restoration. They state that *Benthosuchus*, *Wetlugasaurus*, *Capitosaurus*, and probably *Mastodonsaurus* form a genetically related group. *Rhinesuchus* is related to *Benthosuchus* through *Wetlugasaurus;* the latter was originally described as a *Benthosuchus* but it is distinguished by the less chondrified condition of the neurocranium, the greater length of the rami of the pterygoid, the larger area of denticles on the palatal bones, and the shorter and wide skull. *Benthosuchus* has certain primitive characters in comparison with typical Triassic Stereospondyls, as long rami of the pterygoids, articulation for the lower jaws posterior to the posterior edge of the skull, etc., but there is an equal degree of chondrification of the neurocranium, perhaps due to an early resumption of an aquatic habit. The same precocious chondrification of the neurocranium occurs in the Lower Permian *Trimerorachis*, equaling in degree that of Upper Permian Rhachitomi.

COCHLEOSAURIDAE

This family has been confused with the Melosauridae, practically the same genera being included whichever family name was used. Smith-Woodward included in the Cochleosauridae *Melosaurus* (of Fritsch *non* v. Meyer) as a synonym of *Cochleosaurus*, *Gaudrya*, *Nyrania*, and ? *Phrynosuchus*. All of these have been otherwise referred or declared indeterminate.

Cochleosaurus (fig. 84*A*, 85*A*, *B*) was put in the Melosauridae (Kuhn) and the Cochleosauridae

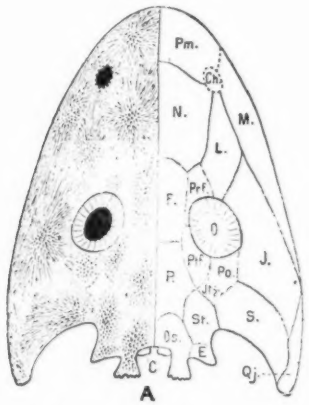

FIG. 84. *Cochleosaurus*. Huene.

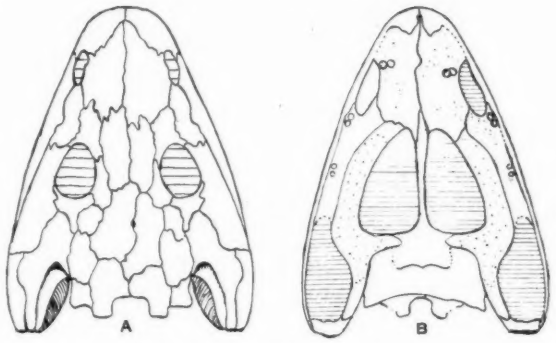

FIG. 85. *Cochleosaurus*. Steen.

(Smith-Woodward, Broili, Romer). Steen (1938) regarded *Melosaurus bohemicus*, *Cochleosaurus falax*, *Dendrerpeton pyriticum*, and possibly *Cochleosaurus deprivatum* as synonyms of *C. bohemicus*. The characters of the family and genus are:

9. Skull depressed; occipital condyle double, ossified with age; pineal foramen disappearing with age; interpterygoid vacuities moderate.
10. Orbits medium size; midlength of skull.
12. Nares. External nares elongate, lateral, well back. Internal nares large, elongate, lateral.
14. Cornua (lappets of Steen) on dermosupraoccipital, increasing in size with age.
15. Intertemporal and supratemporal present.
16. Otic notch large.

DISSOROPHIDAE

The family includes two subfamilies—the Dissorophinae, with the otic notch converted into a complete ring, and the Aspidosaurinae, with the otic notch open. The characters of the family are:

9. Skull short, high or not greatly depressed.
10. Orbits large, midlength of skull.
16. Otic notch large lateral, open or closed in a ring.

The Dissorophinae includes *Cacops*, *Dissorophus*, and ? *Zygosaurus*. The Aspidosaurinae includes *Aspidosaurus*, *Alegeinosaurus*, and *Broiliellus*.

Otocoelus is a synonym of *Dissorophus; Zygosaurus* is questionably a synonym of *Cacops*, and has been, according to Kuhn, confused with *Melosaurus* and *Onchiodon*.

DISSOROPHINAE

Cacops has not been analyzed as the sutures of the skull cannot be made out. The characters are:

1. Body short and stout.
2. Tail short.
3. Limbs strong; carpus and tarsus ossified.
4. Girdles well developed.

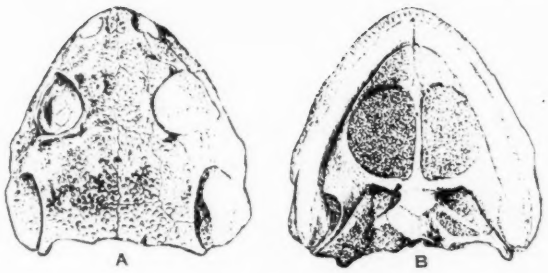

FIG. 86. *Broiliellus*. Williston.

5. Vertebrae with dorsal plates little broader than the vertebrae.
6. Ribs strong, double headed.
7. Sculpture, irregular pitting.
9. Skull high, short, broad, posterior edge concave; occipital condyle double; sensory canals absent; interpterygoid vacuities large; parasphenoid sutured to pterygoid; parasphenoid process slender, almost vestigial.
10. Orbits large, lateral, midlength of the skull.
11. Teeth conical, isodont; tusks on prevomer and palatines.
12. Nares. External nares large, terminal. Internal nares large, oval, lateral.
14. Cornua absent.
16. Otic notch closed.

Dissorophus is accepted by all. *Otocoelus* is regarded as a synonym.

1–4. Probably as in *Cacops*.
5. Vertebrae with dorsal plates transversely elongate, covering much of the body.
16. Ribs double headed.
7. Sculpture irregular pittings.
9. Skull high, short, broad posteriorly, snout obtuse; posterior edge concave; parasphenoid process slender. The skull has not been analyzed as the sutures cannot be made out.
10. Orbits medium to large, round, widely separated; midlength of the skull.
11. Teeth small, isodont, more numerous than in *Cacops;* tusks on prevomers and palatines.
12. Nares. External nares large, oval, nearly terminal. Internal nares long, narrow.

Zygosaurus is "extraordinarily like *Cacops*" (Watson). No restoration of the skull has been attempted. It has minor differences:

9. Skull deeper in the jugal region.
10. Orbits more posterior.
16. Otic notch shorter.

ASPIDOSAURINAE

Alegeinosaurus is known from portions of the axial skeleton only. The characters are:

3. Limbs well developed; carpus and tarsus ossified.
4. Girdles well developed, resemble those of *Cacops*.
5. Vertebrae with expanded, rugose spines; a transversely narrow dermal plate over each spine, not fused with spine; plates shallow V-shaped, imbricate.
6. Ribs with "uncinate" process.
9. Skull unknown.

Aspidosaurus has not been restored. The characters are:

5. Vertebrae with shallow, roof-shaped, transversely narrow dermal plates, fused with spines, imbricate.
9. Skull elongate, triangular, snout rounded.

Broiliellus (fig. 86*A*, *B*) is accepted by all. The characters are:

7. Sculpture "numerous tuberculate tuberosities."
9. Skull subtriangular, broader than long, snout rounded; palate as in *Cacops*, with large interpterygoid vacuities.
10. Orbits large, round, in anterior half of skull.
11. Teeth. Denticles on palatine and prevomer.
12. Nares. External nares large, terminal.
13. Lachrymal extends from orbit to naris.
16. Otic notch large, not closed.

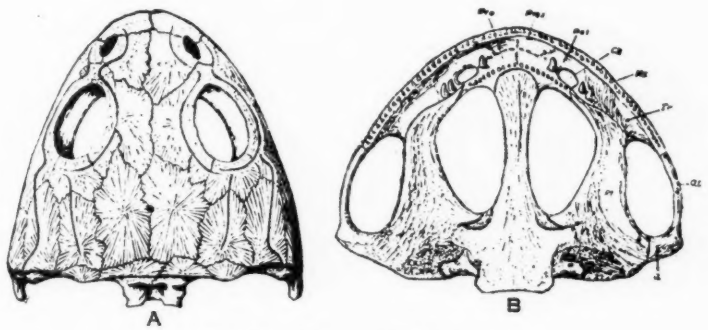

FIG. 87. *Dwinasaurus*. Bystrow.

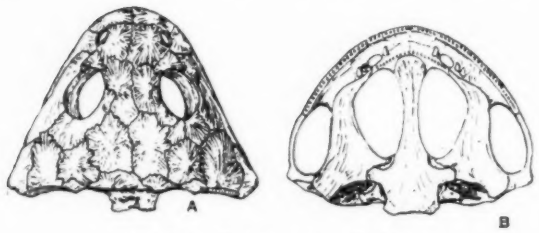

FIG. 88. *Dwinasaurus*. Sushkin.

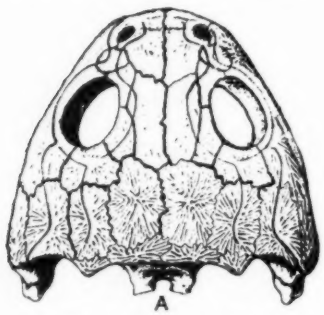

FIG. 89. *Dwinasaurus*. Kuzmin.

DWINASAURIDAE

This family with the single genus, *Dwinasaurus*, is credited by Kuhn to Amalitzki (1921) but occurs as Fam. nov. in Watson's 1919 paper. The characters of the family and genus (fig. 87*A*, *B*, 88*A*, *B*, 89*A*) are:

7. Sculpture radial not pitted.
9. Skull high, or broad and flat (Smith-Woodward); occipital condyles posterior to the posterior edge of the skull; posterior edge of skull oblique, about 45°; parasphenoid movably articulated to the pterygoid, basipterygoid process not obvious; anterior palatal vacuities absent; sensory canals obvious; interpterygoid vacuities large.

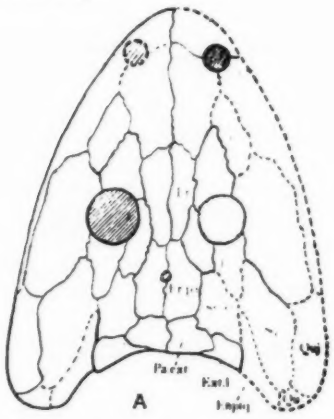

FIG. 90. *Sclerocephalus*. Säve-Söderberg.

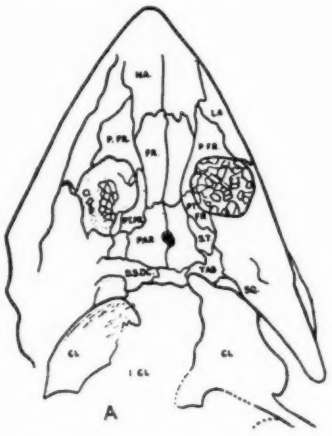

FIG. 91. *Sclerocephalus*. Steen.

10. Orbits large, midlength of skull, or anterior to that point.
11. Teeth. Tusks on palatine and ectopterygoid; denticles on most of the palatal bones.
12. Nares. External nares small, widely separated. Internal nares small, widely separated.
13. Lachyrmal not touching orbit or nares.
14. Cornua slight or absent.
15. Intertemporal and postorbital possibly originally separate as indicated by sculpture.
16. Otic notch absent.

The Dwinasauridae have been compared to both the rhachitomous Plagiosauridae and the sterospondylous Brachyopidae, Efremov going so far (1927) as to refer to *Dwinosaurus* as the most ancient and primitive of the Brachyopidae and (1935) as the "rhachitomous Brachyopid." Nilson, however (1938), denies any phylogenetic relationship and considers the similarity to be due to adaptive parallelism.

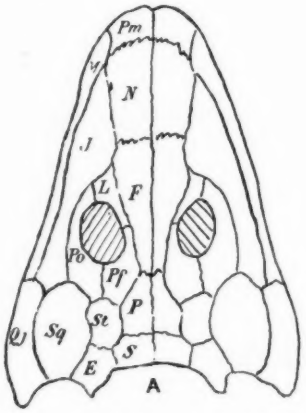

FIG. 92. *Chelydosaurus*. Huene.

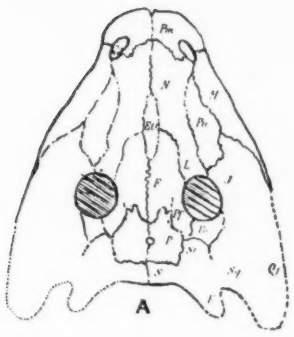

FIG. 93. *Osteophorus*. Huene.

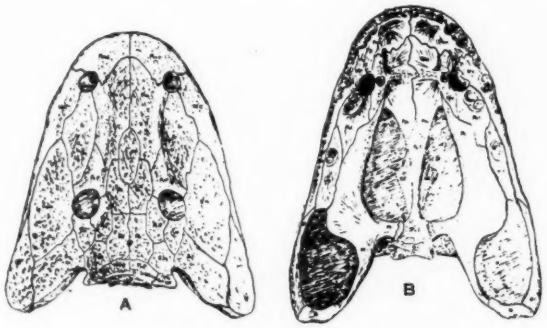

FIG. 94. *Eryops*. Broom.

ERYOPIDAE

This family is close to if not identical with the Actinodontidae. As explained under the discussion of the Actinodontidae, the characters proposed for its separation may well be those of growth stages. Many names proposed for members of this family may be discarded as synonyms, as *Epicordylus*, *Anisodexis*, *Rhachitomus*, and *Parioxys*, all based on fragmentary material from Texas. Other genera referred to the Eryopidae are *Sclerocephalus* (fig. 90*A*, 91*A*), and *Chelydosaurus* (fig. 92*A*) (also referred to the Actinodontidae), *Onchiodon*, *Weissia*, ? *Nyrania* (as a synonym of *Sclerocephalus*), *Phanerosaurus* (now regarded as a reptile), *Osteophorus* (fig. 93*A*) (also referred to the Actinodontidae), *Eryopsoides* (based on fragmentary material), and *Edops* (if this is finally referred to the Eryopidae). More questionably *Stephanospondylus* (now regarded as a reptile), *Melosaurus* (referred to 5 families), and *Chalcosaurus* (referred to 3 families) have been referred to the Eryopidae.

Eryops (fig. 94*A*, *B*, 95*A*, 96*B*, *C*) has the characters of the family. They are:

1. Body stout.
2. Tail moderately long.
3. Limbs strong; carpus and tarsus ossified.
4. Girdles strong; clavicles not expanded proximally; bones of pelvis coössified.
7. Sculpture small pits.
8. Scutes hexagonal, large.
9. Skull not flat, occipital region elevated; occipital condyle triple; basisphenoid movably articulated to pterygoid; pterygoids reach prevomer; interpterygoid vacuities large; septomaxillary and interfrontal present.
10. Orbits small, separated, in posterior half of the skull.
11. Teeth with simply infolded dentine; tusks on prevomer, palatine, and actopterygoid.
14. Cornua absent.
16. Otic notch short or absent.

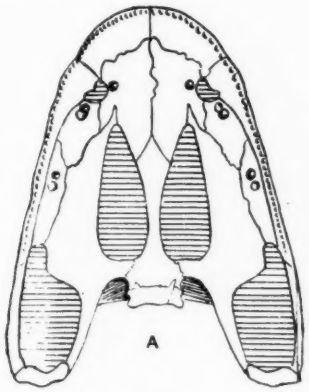

FIG. 95. *Eryops*. Watson.

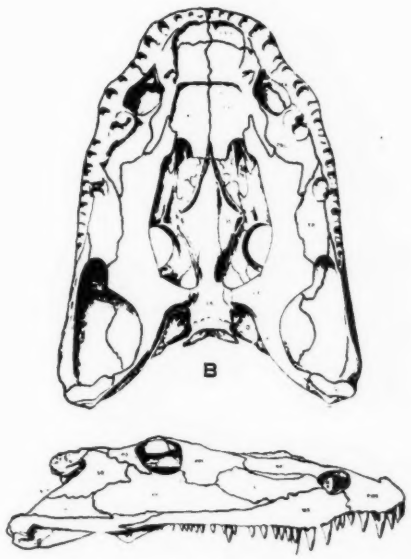

FIG. 96. *Eryops*. Sawin.

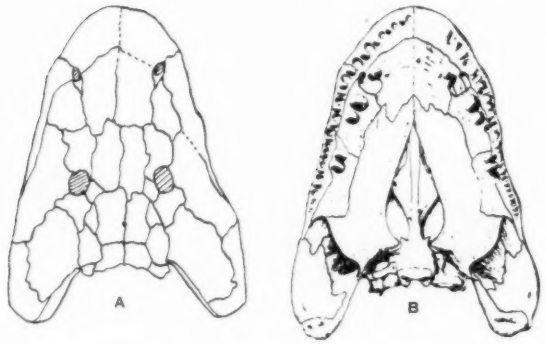

FIG. 97. *Edops*. Romer and Witter.

Edops (fig. 97*A*, *B*) is regarded by Romer and Witter as of Stephanian age. Though Romer does not assign it to the family Eryopidae, he speaks of it as a very primitive member of the Rhachitomi comparable to *Eryops* and *Actinodon*. The characters are:

1. Body like *Eryops* but larger; skull a yard in length.
3. Limbs well developed but not so heavy as in *Eryops*.
7. Sculpture as in *Eryops*.
8. Scutes probably present as they occur in association with fragments of *Edops;* lens-shaped with an average diameter of 8–10 mm.
9. Skull large, proportions as in *Eryops;* articulation of the lower jaw far behind the occipital condyle; condyle round, concave, tripartite; sensory grooves absent; no median interfrontonasal; septomaxillary surficial, i.e., sculptured; anterior palatal vacuities absent; pterygoid articulated movably to parasphenoid; interpterygoid vacuities relatively smallest of all the Rhachitomi; pterygoids meet in suture anteriorly, ventral to the anterior end of the process of the parasphenoid; epipterygoid large.
10. Orbits in posterior half of the skull.
11. Teeth. Tusks on ectopterygoid, palatine, and prevomer; denticles on all palatal bones.
12. Nares. External nares large, well back. Internal nares large, well back, widely separated.
13. Lachrymal nearly touches naris, excluded by septomaxillary.
14. Cornua small.
15. Intertemporal present.
16. Otic notch small.

Romer and Witter remark that *Edops* is essentially Carboniferous rather than Permian in the stage of its development and note the following primitive characters which they say were presumably present in the ancestors of the Rhachitomi while still in the Embolomerous stage of evolution. Though primitive in many characters, it is in others advanced beyond the stage of *Eryops*, as in the greater degree of chondrification of the paroccipital and the supraoccipital.

Edops was more primitive than typical Rhachitomi in:

1. Presence of the intertemporal.
2. Retention of sculpture on the septomaxillary.
3. Movable articulation of the basipterygoid processes with the pterygoids.
4. Unusually small interpterygoid vacuities.
5. Pterygoids meet in an anterior symphasis.
6. Unusually well developed epipterygoids.
7. Less platybasic brain case, with which is associated—
8. A deep pituitary fossa, and
9. A single occipital condyle.

The form most comparable with *Edops* is *Dendrerpeton* from the South Joggins locality in Nova Scotia. Both have a single occipital condyle, with a movable articulation of the pterygoid to the basipterygoid process, and small interpterygoid vacuities. In the same category with *Edops* and *Dendrerpeton* is *Cochleosaurus*, which has the intertemporal present and the lachrymal barely excluded from the orbit. Romer and Witter considered *Trimerorhachis* as a "degenerate side branch of the *Edops* stage." *Edops* is considered as a "late survival of a group of Pennsylvanian ancestral Rhachitomi."

LYDEKKERINIDAE

This family is accepted by all.

Lydekkerina (fig. 98*A*, *B*) is accepted by all. *Bothriceps* is generally regarded as a synonym. The characters of the family and genus are:

4. Girdles. Thoracic girdle well developed; pubis unossified.
9. Skull rather depressed, snout sharply rounded; occipital condyle double; parasphenoid suturally united to the pterygoid; basioccipital ?

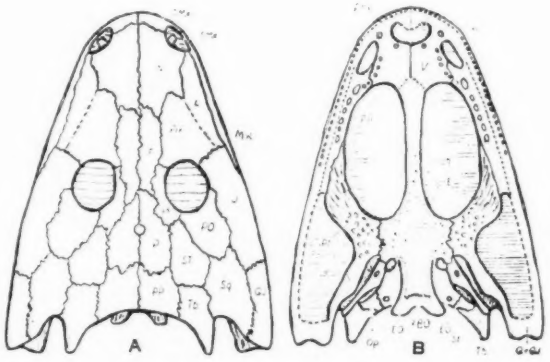

FIG. 98. *Lydekkerina*. Broili.

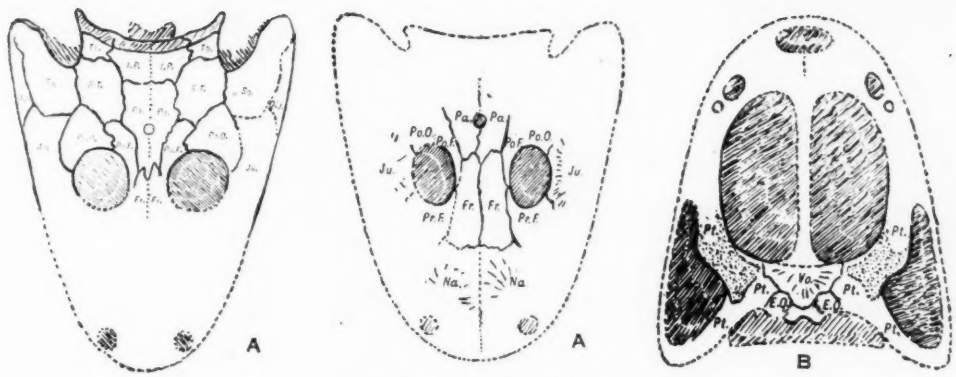

FIG. 99. *Putterillia*. Broom.

present; anterior palatal vacuity single, good-sized; interpterygoid vacuities large (largest proportionally of the Rhachitomi); sensory canals a series of pits; septomaxillary present.

10. Orbits small, in midlength of skull, widely separated.
11. Teeth. Large teeth in double row on parasphenoid and pterygoid; denticles on all palatal bones; all teeth in anterior half of skull.
12. Nares. External nares oval, lateral, nearly terminal.
13. Lachrymal does not touch naris.
14. Cornua formed by tabular, long, slender.
16. Otic notch shallow.

Putterillia (fig. 99*A*, *A*, *B*) is very close to *Lydekkerina*. Its distinguishing characters are:

4. Girdles. Clavicles large, broad; interclavicles short, broad, possibly "very different" (Broom 1930) from *Lydekkerina*.
9. Skull. Nose broader than in *Lydekkerina*; frontal large, twice as long as broad; whole pattern of top little different from *Lydekkerina:* basisphenoid has wide suture with exoccipitals; pterygoids sutured with exoccipitals.
10. Orbits. Whole anterior margin of orbit formed by prefrontal.
11. Teeth. Denticles on pterygoid, not on parasphenoid.

MELOSAURIDAE

This family has been largely abandoned in favor of the Cochleosauridae.

MICROPHOLIDAE

This family has been accepted by all. Watson regarded *Petrophryne major* as a Stereospondyl, Kuhn placed it as a synonym of *Bothriceps*. Smith-Woodward includes *Rhinosaurus* of F. v.W. in the family with question.

Micropholis (fig. 100*A*, *B*) with its synonym *Petrophryne*, from the Procolophon Zone, Rhenosterberg,

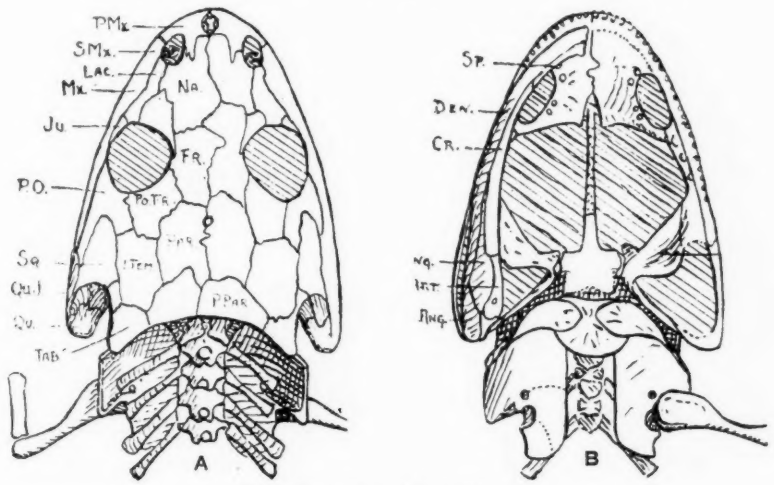

FIG. 100. *Micropholis*. Watson.

Cape Province, South Africa, has the characters of the family. They are:

1. Body small.
7. Sculpture tuberculate, "granular."
9. Skull elongate, depressed; posterior edge concave; occipital condyle double; basioccipital present; sensory canals absent; septomaxillary present; interpterygoid vacuities very large; anterior palatal vacuities separate or nearly so; an internasal bone, homologous with the interrostral, present in a vacuity; supratemporal very small, between squamosal, tabular, and intertemporal.
10. Orbits round, small or medium, in midlength of skull (Smith-Woodward). Orbits large, lateral or medium, in anterior half of skull (Watson).
11. Teeth. Jaw teeth small, dentine not infolded; large teeth on prevomer; a double row on process of parasphenoid; 3 large teeth on slender palatine; denticles on parasphenoid, prevomer, and pterygoid; parasphenoid articulates movably with pterygoid; ectopterygoid "apparently" absent.
12. Nares. External nares oval, anterior, medium size.
13. Lachrymal extends from orbit to naris.
14. Cornua formed by tabular, short, blunt.
15. Intertemporal absent (Watson), but see above.
16. Otic notch large, deep.

NYRANIDAE

This family is most uncertain; the genius *Nyrania* for which it was proposed has been placed in the Melosauridae (Fritsch), Cochleosauridae (Smith-Woodward), Nyranidae (Lydekker and Moodie—the latter considered it as a Microsaur), family *incertae sedis* (Watson).

Nyrania (fig. 101*A*, *B*) has the characters:

8. Skull bluntly triangular; no anterior palatal vacuities.
10. Teeth. Tusks on prevomer, palatine, and ectopterygoid. Denticles on all palatal bones.

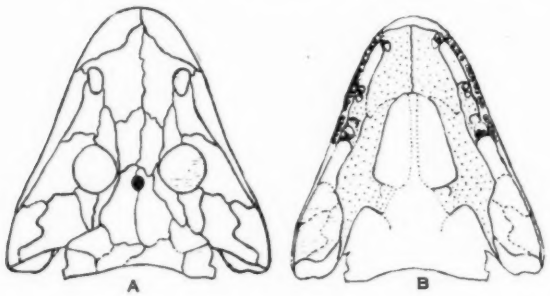

FIG. 101. *Nyrania*. Steen.

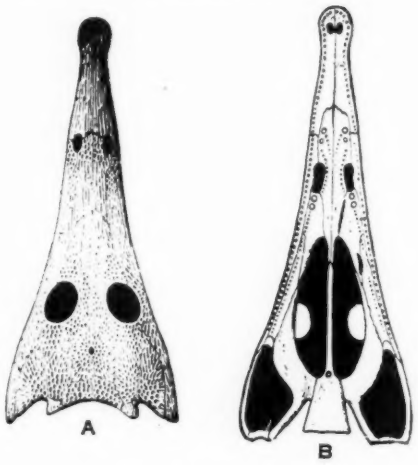

FIG. 102. *Platyops*. Bystrow.

12. Nares. External nares well back, elongate, oval. Internal nares elongate, lateral.
13. Lachrymal not touching orbit.
16. Otic notch well defined.

PLATYOPIDAE

This family name was proposed by Huene (1931) but not defined. It was adopted by Kuhn to include the genus *Platyops* only. The *Platyops* of Twelvetrees (non Williston) was regarded by Lydekker (1889) as a member of the Anthracosauridae, but on page XI of the Addenda and Corrigenda of Nicholson and Lydekker, *Paleontology*, Vol. 11, he suggested the name *Platyposaurus* for *Platyops* preoccupied, and said that it should be placed in the Archegosauridae because "the vertebrae are rhachitomous." However Neave does not list the Platyops of Twelvetrees as preoccupied. The genus was put in the Eryopidae (Smith-Woodward) and *incertae sedis* (Watson).

Platyops (fig. 102*A*, *B*, 103*A*) (*Platyposaurus*) was based on a fragmentary skull, some vertebrae, limbs bones and scales. It is so little understood that it is best placed, with Watson, as *incertae sedis*.

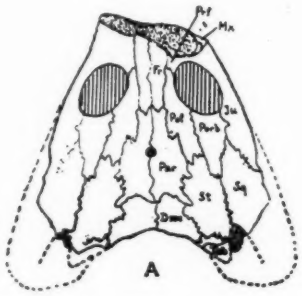

FIG. 103. *Platyops*. Efremov.

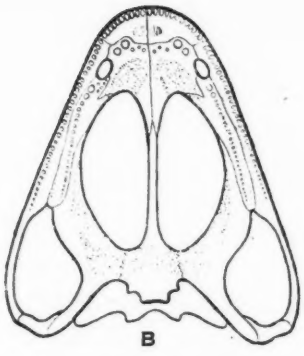

FIG. 104. *Rhinesuchus*. Bystrow and Efremov.

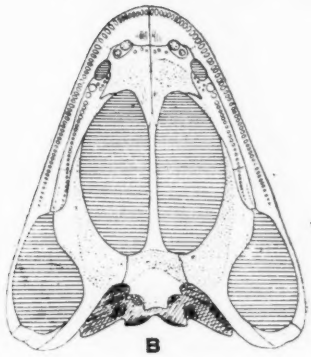

FIG. 105. *Rhinesuchus*. Watson.

RHINESUCHIDAE

This family, with the exception of the very dubious suggestion that *Gondwanosaurus* from India is a member, is accepted by all. Its characters are:

9. Skull depressed; pterygoids do not reach the prevomers; interpterygoid vacuities large; parasphenoid sutured to the pterygoid; occipital condyle double.
10. Orbits far back, small.

Rhinesuchus (fig. 104*B*, 105*B*) has the characters:

9. Skull depressed basioccipital large, perforate, deeply cupped, separating exoccipital condyles; interpterygoid vacuities large; anterior palatal vacuities absent or small; parasphenoid sutured to the pterygoid; pterygoids do not reach the prevomers.
10. Orbits small, far back.
11. Teeth. Tusks on prevomers; denticles on prevomer, palatine, and parasphenoid; a palatal row paralleling the maxillary row.

Rhinesuchoides has the characters:

9. Skull exceptionally long and narrow; arrangement of roof bones as in *Rhinesuchus*.
11. Teeth as in *Rhinesuchus*.

The new genus was proposed on the basis of the proportions of width to length:

Rhinesuchoides 1:2 *Rhinesuchus* 5:6 and 4:5

This may easily prove to be but the result of growth.

Gondwanasaurus (fig. 106*A*, *B*, *C*) was based on a skull and parts of a skeleton. The skull is an internal cast from which the bone has been largely denuded; Lydekker restored the sutures in dotted line after the pattern of *Mastodonsaurus*. It was placed in the Rhinesuchidae (Smith-Woodward, Kuhn) and in the Stereospondyli, probably indeterminate (Watson). The material does not permit critical determination.

Laccosaurus was based on a skull lacking the antorbital region. The character distinguishing it from *Laccocephalus* is the presence of denticles upon the palatal bones.

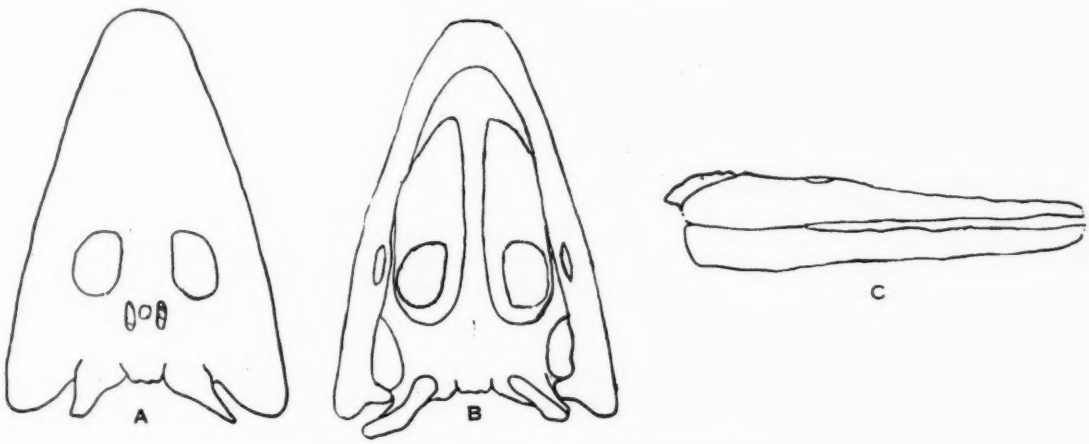

FIG. 106. *Gondwanasaurus*. After Lydekker.

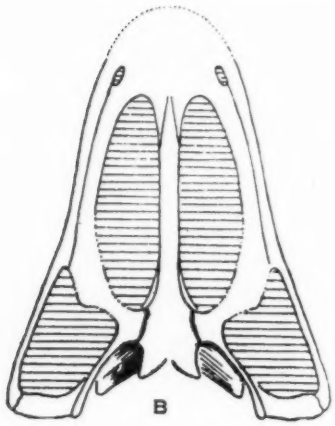

FIG. 107. *Laccocephalus*. Watson.

Laccocephalus (fig. 107*B*) was based on a left half and part of a right half of a skull. Its characters are

9. Skull with the basisphenoid a large well ossified element present on top of the parasphenoid; parasphenoid sutured to the pterygoid; epipterygoid said to be sutured to the pterygoid; interpterygoid vacuities large.
11. No denticles on the palatal bones.
16. No otic notch.

Uranocentrodon (fig. 108*A*, *B*) (for *Myriodon* preoccupied), is possibly synonymous with *Rhinesuchus* (Huene, Piveteau). The characters are:

8. Scutes present, elongate on abdomen, round on back.
9. Skull. Pattern of the roof bones much like that of *Lydekkerina*, resemblance in postorbital region "almost exact."
10. Orbits small, oval, on top, not widely separated.
11. Teeth. Denticles on all palatal bones.
13. Lachrymal does not touch either orbit or naris.
14. Cornua formed by tabular, strong, "very marked."
16. Otic notch moderate.

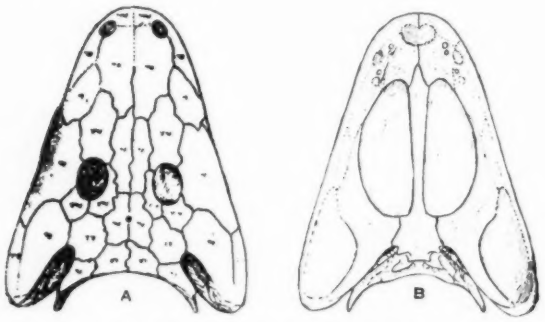

FIG. 108. *Uranocentrodon*. Broom.

Watson (1916) says that *Uranocentrodon* is exactly intermediate between *Eryops* and the Triassic Stegocephalians in the reduction of the basisphenoid and parasphenoid and parts of the axial skeleton. Evidence of convergent evolution is present in the series *Eryops-Uranocentrodon*—the Triassic Stegocephalia, and *Ceraterpeton-Batrachiderpeton-Diplocaulus*. Both series were influenced by the return from a terrestrial to aquatic life.

TREMATOPSIDAE

This family has the single genus *Trematops* although other genera have been tentatively suggested as members. The characters of the family are those of the genus.

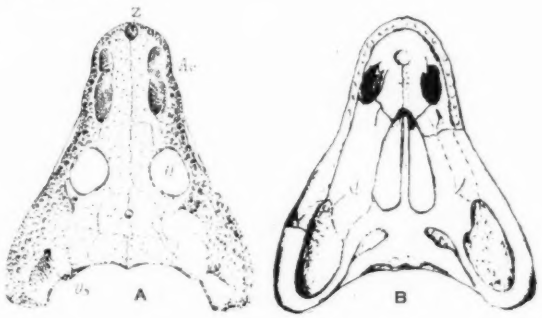

FIG. 109. *Trematops*. Broili.

Trematops (fig. 109*A*, *B*) is accepted by all. The characters are:[12]

1. Body probably short and stout.
3. Limbs short and strong; tarsus and probably carpus well ossified.
4. Girdles well developed; bones of pelvis coossified as in *Eryops*.
7. Sculpture, irregular pittings.
9. Skull high, muzzle contracted; an inter-premaxillary vacuity present, but no bone; large antorbital vacuities connected with the nares; interpterygoid vacuities medium-sized; no defined basipterygoid process; parasphenoid vestigial or absent; occipital condyle ? tripartite, posterior edge of skull concave, lower jaw articulation back of condyle.
10. Orbits near midlength of the skull.
11. Teeth nearly isodont, enlarged anterior maxillary teeth; two tusks on palatine, one on prevomer.
14. Cornua absent.
16. Otic notch closed; elongate antero-posteriorly, small opening.

TRIMERORHACHIDAE

This family is accepted by all. The characters are those of the genus *Trimerorhachis*.

[12] See footnote to *Acheloma*, page 372.

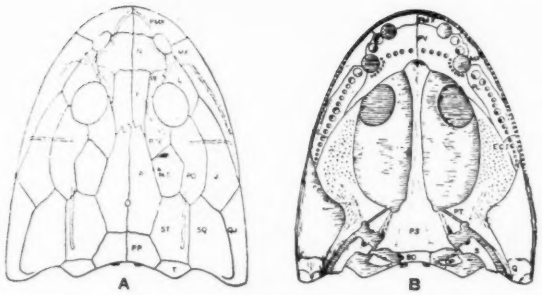

FIG. 110. *Trimerorhachis*. Case.

Trimerorhachis (fig. 110*A*, *B*) has the characters:

1. Body stout, salamander-like.
2. Tail medium-length; vertically compressed.
3. Limbs fairly strong; carpus and tarsus cartilaginous.
4. Girdles well developed; pubis cartilaginous.
5. Vertebrae typically rhachitomous.
6. Ribs slender, curved, single-headed.
7. Sculpture irregular pitting.
8. Scutes abundant, oat-shaped, imbricate; cartilaginous or calcified, not ossified; covering body.
9. Skull depressed; occipital condyle single, tripartite; interpterygoid vacuities large; parasphenoid large; basioccipital not obvious; parasphenoid articulates movably with the pterygoid; sensory canals obvious; anterior palatal vacuities small, separated, far forward; septomaxillary perhaps present.
10. Orbits small, in anterior half of the skull.
11. Teeth. Premaxillary and maxillary teeth small, isodont, conical, simple infolding of dentine. Tusks on prevomer and palatine; large teeth on ectopterygoid continuous with those on the palatine; denticles on pterygoid.
12. Nares. External nares small, oval, oblique, separated, not terminal. Internal nares medium size, round, separated.
13. Lachrymal extending from orbit to nares.
14. Cornua absent.
15. Intertemporal present.
16. Otic notch absent.

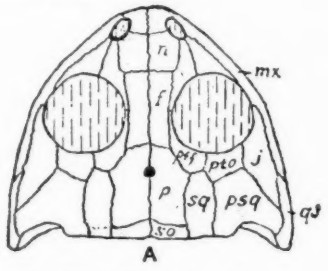

FIG. 111. *Tersomius*. Case.

Tersomius (fig. 111*A*) was based on a single small skull resembling *Trimerorhachis* in most particulars but distinguished by characters:

9. Skull more roundly triangular.
10. Orbits large; midlength of skull or slightly anterior.
11. Teeth. No tusks or enlarged teeth.
15. Intertemporal absent.

ZATRACHYDAE

This family, with its variant spellings (Zatrachydidae Kuhn, Zatrachysidae Smith-Woodward, Zatrachidae Romer), includes several genera. The limits of the family may be altered with increased knowledge as the specimens occur from the Allegheny Formation, Pennsylvanian to the Permian, of Kenilworth, England.

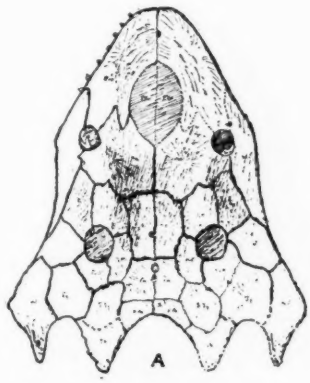

FIG. 112. *Zatrachys*. Broom.

Zatrachys (fig. 112*A*) has the characters of the family and genus; they are:

9. Skull flat; a ridge from the orbit to the nares leaving the midline sunken; large internasal vacuity but no internasal bone; antorbital pits present; edges of the skull serrate; interpterygoid vacuities small; prevomers "enormous" (Broom 1913) forming anterior half of the palatal surface; septomaxillary present.
10. Orbits relatively small, far back.
11. Teeth. Denticles on all palatal bones; no tusks in evidence.
12. Nares. External nares well back, edges elevated.
13. Lachrymal does not reach naris.
14. Cornua well developed, present on tabular and quadratojugal.
15. Otic notch small, or well developed.

Platyhistrix (fig. 113*A*) is accepted by all as a member of the Zatrachydae. *Ctenosaurus rugosus* is recognized as a synonym.

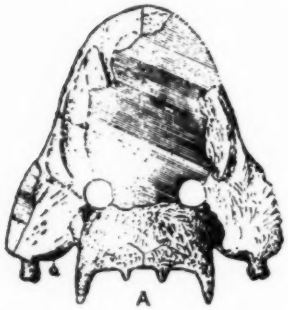

FIG. 113. *Platyhistrix*. Williston.

5. Vertebrae with thin elevated spines with the surface tuberculate.
8. Skull with four projections backward from the posterior edge of the cranial table, and a strong projection from the squamosal.

Williston figured a skull (1916) and says in his description "Skull with four projections backward from the cranial table, the tabular projection conical and slender. A projection from the outer side of the quadrate."

15. Cornua. Probably certain of the projections are cornua.

Dasyceps (fig. 114*A*) is placed by all in the Zatrachydae. The characters are:

9. Skull with a large internasal vacuity, possibly an internasal bone; edges of skull serrate; squamosal possibly bipartite; jugal takes little part in the orbits; nasal large and broad; anterior palatal vacuities present directly under the intermaxillary vacuity.
10. Orbits small, in the posterior half of the skull, widely separated.
11. Teeth. Denticles on the prevomer and palatine.

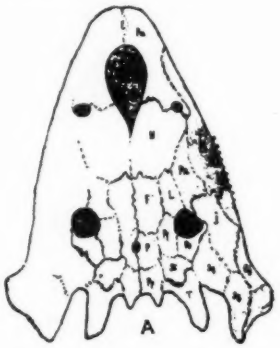

FIG. 114. *Dasyceps*. Huene.

12. Nares. External nares small, well back. Internal nares large.
13. Lachrymal reaches from orbit almost to the naris.
14. Cornua formed by tabular, large; a lesser projection on the dermosupraoccipital, and a larger on the squamosal (? quadratojugal).
16. Otic notch deep.

Stegops (fig. 115*A*, *B*, *C*) has long been regarded as a member of the Phyllospondyli or the Lepospondyli but has been shown by Steen and Romer to belong in the Rhachitomi, in which case it must belong in or near to the family Zatrachydae. Romer regarded *Ceraterpeton* and *Erpetosaurus* as synonyms of *Stegops*. In referring to Moodie's family Stegopidae, Romer said (1930) that only *Stegops*, *Platyrhinops* (*Tuditanus mordax*), and possibly *Platystegops*, belong in the family. He regarded this group as closely related to the Permian forms *Acanthostoma*, *Dasyceps*, *Zatrachys*, and *Platyhistrix*, noting that the latter have an internasal vacuity, a greatly developed muzzle, and a lesser development of the tabular cornua (the last two points being questionable). In 1938 after Steen's (1938) demonstration that *Acanthostoma* was a rhachitomous

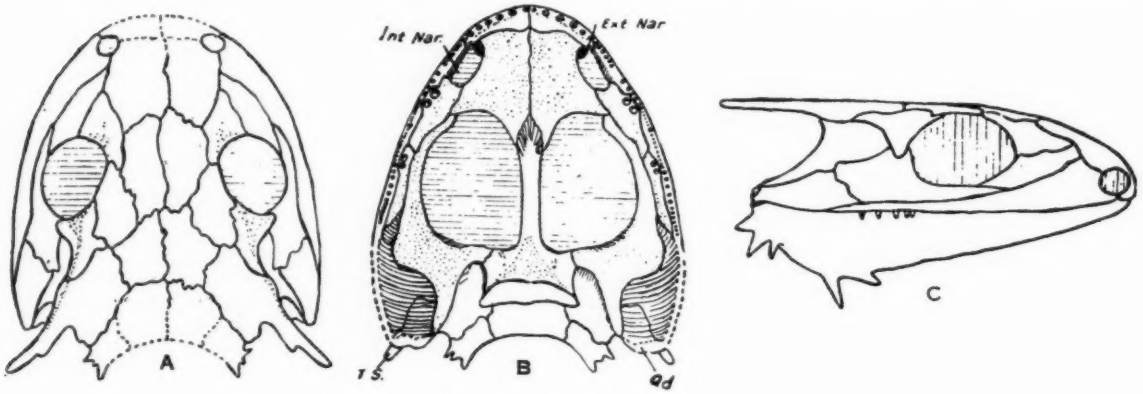

FIG. 115. *Stegops*. Steen.

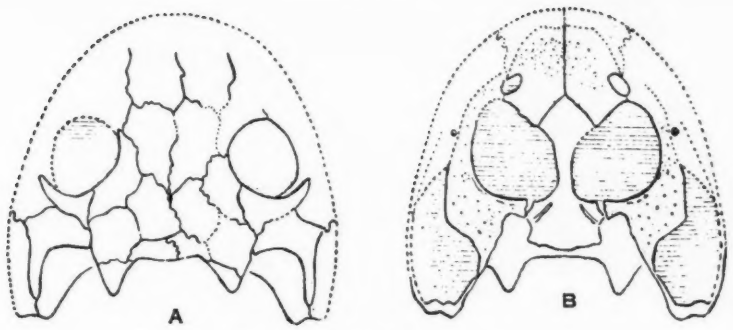

FIG. 116. *Platyrhinops*. Steen.

form, and after his discovery of "certain dubious structures" in the specimen of *Stegops* which might be rhachitomous centra he suggested a series *Stegops-Acanthostoma-Platyhistrix*. It is to be noted that *Stegops* has spiny projections on the angular of the lower jaw.

Platyrhinops (fig. 116*A*, *B* 117*A*, *B*) (for *Tuditanus mordax*) was formerly referred to the Phyllospondyli but Steen (1938) showed it to be rhachitomous, and Romer (1938) remarked that it is "apparently related to *Stegops* and hence presumably rhachitomous." According to Steen (1938) it differs from *Stegops* in the lack of a cornua and the absence of a spine on the supratemporal. The characters, which are largely in common with *Stegops*, are:

7. Sculpture fine, regular pitting.
9. Skull with blunt snout (dotted in Steen's restoration); posterior edge of skull concave; basisphenoid sutured to pterygoid (?? E.C.C.); interpterygoid vacuities broad.
10. Orbits large, in midlength of the skull, widely separated.
11. Teeth. Tusks on the ectopterygoid; denticles on the prevomers, pterygoids and parasphenoid.
12. Nares. Internal nares small, oblique, far back.
14. Cornua formed by tabular, extended (but see Steen above).

There are numerous forms which are in all probability members of the Rhachitomi but of uncertain family relationship.

Callignethelon from the Carboniferous of South Joggins, Nova Scotia.

Calochelys (*Calochelis* by *lapsus*) from the Westphalian of Nyran, Bohemia. No skull known, regarded as a synonym of *Sparagmites*.

Chalcosaurus from the Permian of the Kargalia District of the Urals, Russia, exact location unknown, but in the Cupriferous Yellow Sandstone. Anterior half of a skull of which no figure has been given. Efremov (1937) said that it is either a Branchiosaurid or a Brachyopid, near *Dwinasaurus*, probably the latter. He says that it occurs in beds that "ought to be" older than the Pareiasaurian zone of the North Dwina River.

Dendryazousa Carboniferous of South Joggins, Nova Scotia.

Dendrysekos Carboniferous of South Joggins, Nova Scotia. Based on a specimen called *Dendrerpeton acadianum* by Dawson.

Discosauriscus for *Discosaurus* preoccupied.

Discosaurus from the Lower Permian of the Plauenschengrund near Dresden. Also identified from Bohemia and from the Orenburg region in Russia. The type material contains no skull.

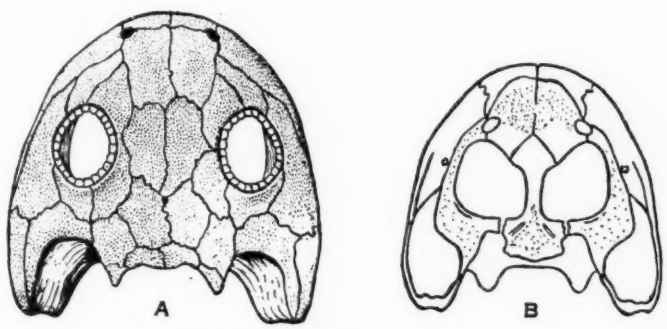

FIG. 117. *Platyrhinops*. Bystrow.

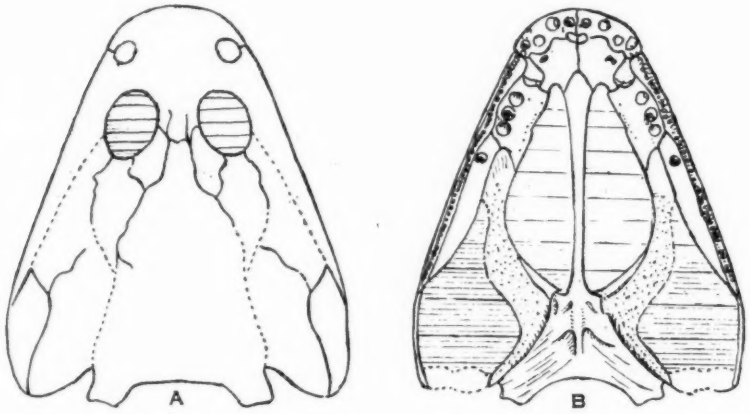

FIG. 118. *Erpetosaurus*. Steen.

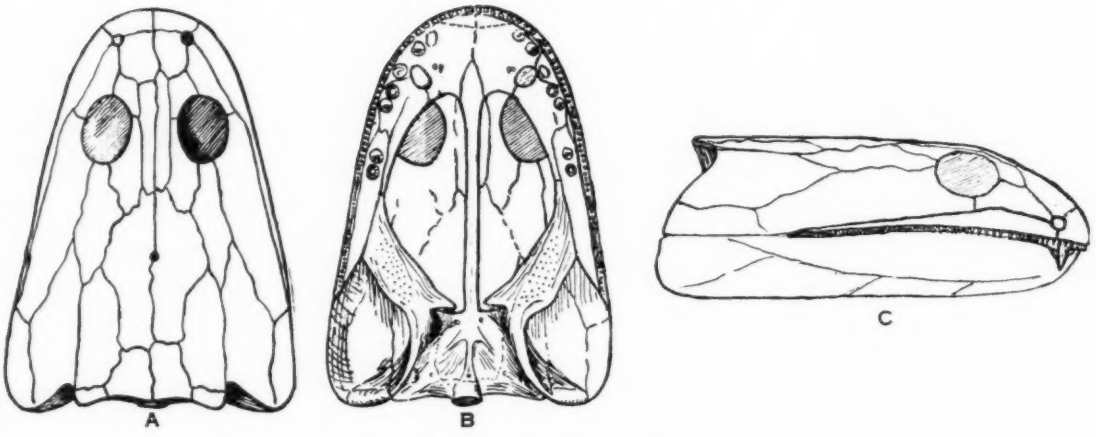

FIG. 119. *Erpetosaurus*. Romer.

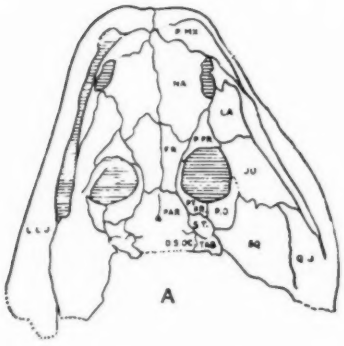

FIG. 120. *Lusor*. Steen.

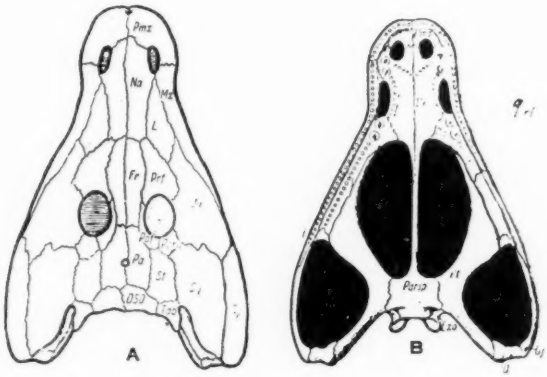

FIG. 121. *Melosaurus*. Efremov.

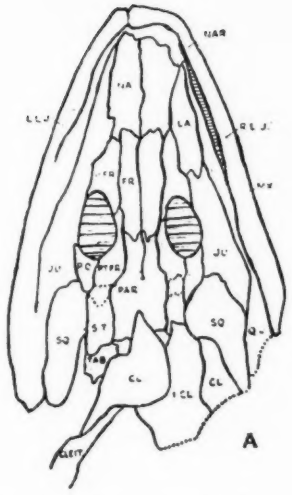

FIG. 122. *Memonomenos*. Steen.

Erpetosaurus (fig. 118*A*, *B*, 119*A*, *B*, *C*). This genus has been largely broken up, but the specimens called *E. radiatus* and *E. laevis* are regarded by Steen as Rhachitomi. The specimens described by Moodie (1916) and Romer are very different things. Moodie's specimen is far nearer to Romer's *Branchiosauravus* (*E. tabulatus*).

Goniocara, for *Goniocephalus* preoccupied, from the Lower Permian of Texas, was described from the posterior end of a small skull. It has variously been placed in the ? Reptilia (Hay), Adelospondyli (Romer) and the Rhachitomi *indet.* (Kuhn).

Goniocephalus synonym of *Goniocara*.

Lusor (fig. 120*A*) from the Upper Rothliegende of Ruprectice near Brounov is placed *incertae sedis* in the Rhachitomi. The characters are:

9. Skull with very short postorbital region; cheeks region as in *Sclerocephalus*, extends back until the jaw articulation is posterior to the occipital condyles.
10. Orbits in the posterior half of the skull.
12. Nares. External nares elongate, not terminal.
13. Lachrymal does not touch orbit.

Melosaurus (fig. 121*A*, *B*) from the Cupriferous Sandstone, Kazanian, of the West Ural region has been placed in four families and *incertae sedis* in the Rhachitomi. The characters, as given by Hartmann-Weinberg, are:

9. Skull with concave sides, narrow snout, and broad temporal region; relatively flat; anterior palatal vacuities oval, small, separate; parasphenoid articulated movably to the pterygoid; basioccipital present.
10. Orbits in the posterior half of the skull.
11. Teeth. A palatal row paralleling the maxillary row.
12. Nares. External nares small, not terminal. internal nares kidney-shaped.
13. Lachrymal touches neither the orbit nor naris.
15. Intertemporal absent.
16. Otic notch deep.

Efremov says (1937) "we may possibly regard" *Melosaurus* as closely related to the rhachitomous ancestors of *Mastodonsaurus*. It is not a member of a distinct family but belongs in the Benthosuchidae (Neorhachitomi). He believes *Melosaurus* to be a primitive member of the group including *Capitosaurus* and *Mastodonsaurus*.

Memonomenos (fig. 122*A*) from the Stephanian of Kostlov, Bohemia, is put in the Rhachitomi *incertae sedis* by Steen; it is equivalent to *Callignethelon* and *Dendryazousa* of the Middle Coal Measures of Nova Scotia. Steen gives the characters:

9. Skull long and slender.
14. Cornua small, "a relic."

Phrynosuchus (fig. 123*B*) from the Lower Beaufort, ? Endothiodon zone, of Fraserberg, Cape Province, has been placed in the Melosauridae (Kuhn), Cochleosauridae (Smith-Woodward), Plagiosauridae (Huene), and family indet. (Haughton). Haughton quotes Broom's characterization (1925):

9. Skull broad, very flat; parasphenoid body and process very broad; prevomers and palatines large; interpterygoid vacuities relatively small.
10. Orbits in anterior half of the skull, widely separated.
11. Teeth. Tusks on the prevomer.
12. Nares. External nares widely separate.

Petrobates from the Plauenschengrund near Dresden is regarded as either a Branchiosaurid (Kuhn) or a Hylonomid (Smith-Woodward).

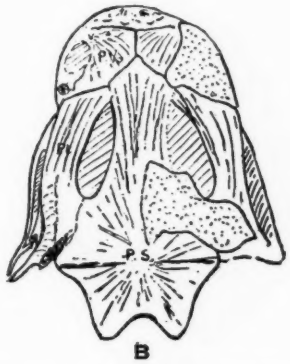

FIG. 123. *Phrynosuchus*. Haughton.

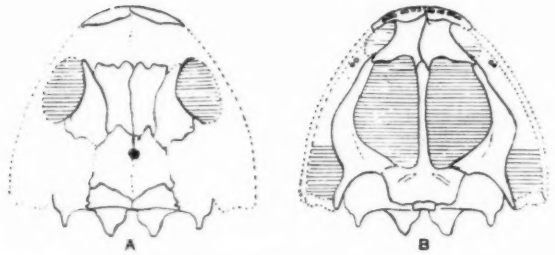

FIG. 124. *Potamochoston*. Steen.

Potamochoston (fig. 124*A*, *B*) from the Westphalian of Nyran is regarded by Steen as a Rhachitomid. The characters are:

9. Skull broad, roundly triangular; parasphenoid articulates movably with the pterygoid; condyles posterior to the posterior edge of the skull; interpterygoid vacuities "exceptionally large."
10. Orbits large, in the anterior half of the skull; sclerotic plates present.
12. Nares. External nares unknown. Internal nares large, oblique, widely separated, nearly lateral.
14. Cornua small.

Platystegos from the Coal Measures of South Joggins Nova Scotia. Moodie gives the characters:

7. Sculpture close, deeply pitted.
9. Skull short, broad.
10. Orbits large.
11. Teeth with infolded dentine, curved, cutting edges at apex; palatine teeth very long; denticles on prevomer.
14. Cornua formed by tabular and squamosal, projecting posterior to occipital condyle (Moodie), or cornua absent (Steen 1934).
15. Intertemporal present.
16. Otic notch good sized.

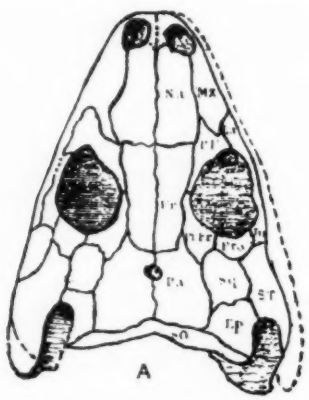

FIG. 125. *Rhinosaurus*. Fritsch.

Rhinosaurus (fig. 125*A*), F. D. Waldheim *non* Marsh, from the Permian of the Simbirsk region, is regarded by Efremov (1940) as possibly "much like" a Pelycosaur. The type is lost and the location and taxonomic position are both very uncertain.

Stephanonsaurus from the Permian of the Plauenschengrund near Dresden has been put in the Diadectidae (Smith-Woodward), Eryopidae as a synonym of *Onchiodon* (Kuhn), and in the Cotylosauria (Case).

Sparagmites from the Westphalian of Nyran and the Permian of the Plauenschengrund near Dresden is not represented by a good skull. It was put in the Archegosauridae (Smith-Woodward, Kuhn), the latter considered *Chalcochelys* as a synonym.

STEREOSPONDYLI

There is greater unanimity of opinion concerning the Sterospondyli than any other group of the Stegocephalia. Nine families have been proposed and most of them have been accepted. They are the

Brachyopidae
Capitosauridae
Mastodonsauridae
Metoposauridae
Peltostegidae
Plagiosauridae (= Brachyopidae)
Rhytidostidae
Trematosauridae
Wetlugasauridae (perhaps Rhachitomi)

All Stereospondyli have the bones of the neurocranium secondarily chondrified to a greater or less degree; the parasphenoid sutured immovably to the pterygoids and exoccipitals; the cornua are always formed by the tabular; the intertemporal bones absent, except in the doubtful case of *Gonioglyptus*. The differences in families and genera are largely in the adaptive characters referable to a greater or less degree of aquatic life and to feeding habits.

LIST SHOWING THE CLASSIFICATION, GEOLOGICAL HORIZON, AND LOCALITY OF THE DETERMINABLE STEREOSPONDYLI

Brachyopidae

Plagiosuchus, Upper Triassic, Lettenkohle, of Wurtemberg, Germany.

Bothriceps, probably from Upper Triassic, Hawksbury, of N.S.W., Australia.

Plagiosaurus, Middle-Upper Triassic, Steuben Sandstone, of Germany.

Plagiosternum, Middle Triassic, Muschelkalk, of Crailsheim, Germany.

Brachyops, Lower Triassic, Mangali Stage, India.

Batrachosuchus, Lower Triassic, Cynognathus zone, Aliwal North, South Africa.

Capitosauridae

Capitosaurus, Upper Triassic, Hawksbury, Australia. Upper Triassic, Lower Keuper, many places

in Germany. Middle Upper Triassic, Rouxville District, South Africa. Middle Triassic, Posidonomya Beds, Spitzbergen. Middle Triassic of Great Bogda Region, South Russia. Lower Triassic, Bunter, of Helgoland and Germany.

Kestrosaurus, Lower Triassic, Procolophon zone, O.F.S., South Africa.

Cyclotosaurus, Upper Triassic, Hawksbury, Queensland, Australia. Upper Triassic, Lower Keuper, England. Middle Triassic, Posidonomya Beds, Spitzbergen. Middle Triassic, Great Bogdo Region, South Russia. Middle Triassic, Muschelkalk, Germany. Lower Triassic, Bunter, Germany.

Mastodonsauridae

Mastodonsaurus, Upper Triassic of England. Upper Triassic of ? India. Lower Triassic, Bunter and Lettenkohle, of Bernberg, Germany.

Heptasaurus, Lower Triassic, Upper Bunter, Baden, Germany.

Metaposauridae

Metoposaurus, Upper Triassic, Middle Keuper, Germany.

Koiskinodon, Upper Triassic, Popo Agie Beds, Wyoming, U.S.A.

Kalamoiketor, Upper Triassic, Chinlee, Arizona, U.S.A.

Buettneria, Upper Triassic, Dockum Beds, Texas, U.S.A.

Borophagus, Upper Triassic, Popo Agie Beds, Wyoming, U.S.A.

Anaschisma, Upper Triassic, Popo Agie Beds, Wyoming, U.S.A.

Rhytidostidae

Rhytidosteus, Lower Triassic, Upper Beaufort Beds, Rouxville District, South Africa.

Trematosauridae

Aphanerama, Upper Triassic, Kampili Calc, Great Bogda Region, South Russia. Middle Triassic, Posidonomya Beds, Spitzbergen.

Lonchorhynchus, Middle Triassic, Posidonomya Beds, Spitzbergen.

Lyrocephalus, Middle Triassic, Posidonomya Beds, Spitzbergen.

Peltostega, Middle Triassic, Posidonomya Beds, Spitzbergen.

Platystega, Middle Triassic, Posidonomya Beds, Spitzbergen.

Stoschiosaurus, Middle Triassic, Posidonomya Beds, Spiztbergen.

Tertrema, Middle Triassic, Posidonomya Beds, Spitzbergen.

Trematosaurus, Lower Triassic, Bunter Sandstone, Germany. Lower Triassic, Volga Region, Russia. Lower Triassic, ? Upper Beaufort, ? O.F.S., South Africa.

Trematosuchus, Lower Triassic, Upper Beaufort, O.F.S., South Africa.

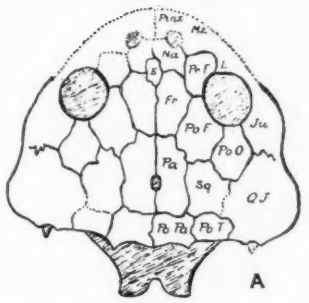

FIG. 126. *Batrachosuchus*. Broom.

Gonioglyptus, Lower Triassic or Upper Permian, Chideru, India.

Microposaurus, Lower Triassic, Upper Beaufort, of Wonderboom, Cape Province, South Africa.

Thoösuchus, Triassic, of Ustyuni town, Russia.

Wetlugasauridae

Wetlugasaurus, Lower Triassic of Wetlugaland, North Russia.

BRACHYOPIDAE

Huene (1922) preferred the name Plagiosauridae because Jaekel (1913) had proposed a group, Plagiosauri, two years before Broom (1915) proposed the family Brachyopidae. The characters of the family are:

9. Skull short, depressed, broad; outer edges of the pterygoids turned down, or arched; i.e., the palate is trough-shaped in relation to the greater development of muscles activating the lower jaw.
10. Orbits large or medium-sized; far forward.

Batrachosuchus (fig. 126*A*, 127*B*, 128*A*, *B*) is placed in this family by all. The characters are:

7. Sculpture of network of "reticulate and radiating" pits and ridges.
9. Skull moderately short and broad; pterygoid with antero-posterior descending flange; no

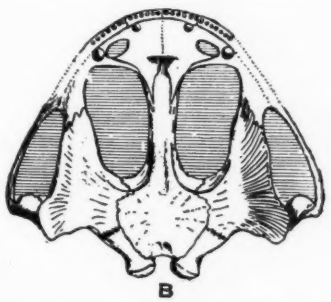

FIG. 127. *Batrachosuchus*. Watson.

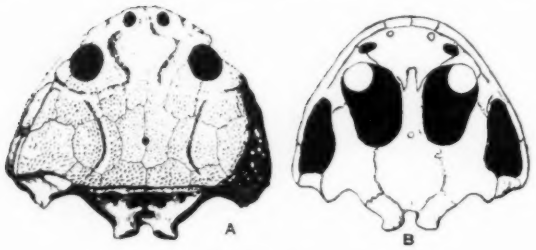

FIG. 128. *Batrachosuchus*. Bystrow.

anterior palatal vacuities observed; an interfrontal present; lyra of sensory canal system strong.

10. Orbits of moderate size, round, far forward, widely separated.
11. Teeth small on premaxillary and maxillary (indicated by author); tusks on prevomer and palatines; palatal row paralleling the maxillary row uncertain.
12. Nares. External nares large, nearly median. Internal nares elongate oval, nearly transverse, separated.
13. Lachrymal uncertain because of condition of the specimen.
14. Cornua absent.
16. Otic notch absent.

Broom suggested the possibility that this genus was rhachitomous because of the fact that intercentra were found in the same bed. Lydekker's *B. huxleyi* is a *Lydekkerina*.

Bothriceps (fig. 129*A*). *B. major* is from the "kerosene shales" of the Upper Division of the Newcastle Coal Measures, probably nearly at the line between the Permian and the Triassic (Watson 1931) David and Süssmilch say that the accompanying plants and insects show the same horizon. Watson in referring to *B. major* says, "Brachyopidae or rhachitomous Dwinasauridae." The characters are:

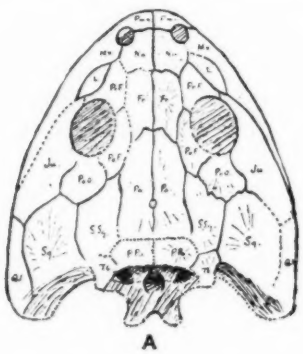

FIG. 129. *Bothriceps*. Broom.

9. Skull longer than broad, narrowed anteriorly; pterygoid rugose near junction with the parasphenoid; occipital surface sloping down and back.
10. Orbits moderate size, round, separated, just anterior to the midlength of the skull.
11. Teeth unknown.
12. Nares. External nares moderate size, anterior, not terminal.
13. Lachrymal touches neither orbit nor naris.
14. Cornua absent.
16. Otic notch present, small.

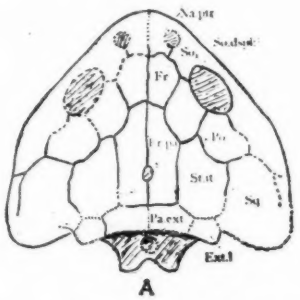

FIG. 130. *Brachyops*. Säve-Söderberg.

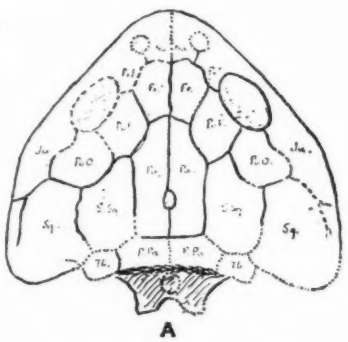

FIG. 131. *Brachyops*. Broom.

Brachyops (fig. 130*A*, 131*A*) has the following characters:

9. Skull large, very broad, bluntly triangular. Lyra of the sensory system faint; occipital region slopes down and back; condyles considerably behind the plane of the quadrates.
10. Orbits widely separated, oval, oblique, in anterior half of the skull.
11. Teeth unknown.
14. Cornua absent.
16. Otic notch small or absent.

The specimen is much injured, showing the inner side of the roof bones. Broom (1915) expressed doubt as to its being distinct from *Bothriceps*.

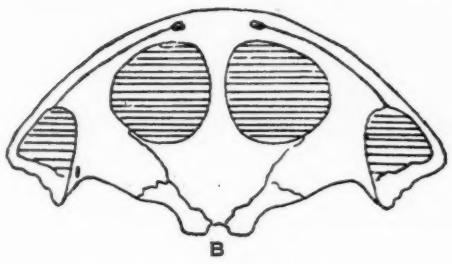

FIG. 132. *Plagiosaurus*. Watson.

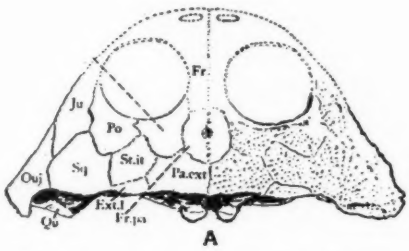

FIG. 133. *Plagiosaurus*. Säve-Söderberg.

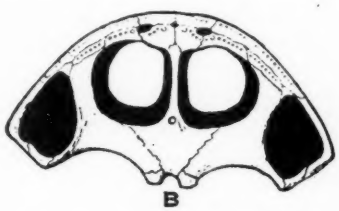

FIG. 134. *Plagiosaurus*. Bystrow.

Plagiosaurus (fig. 132*B*, 133*A*, 134*B*) is regarded by Smith-Woodward as a synonym of *Plagiosternum*, but Kuhn regards it as a distinct genus. The characters are:

9. Skull very broad, interpterygoid vacuities large.
10. Orbits large, close together.
11. Teeth. Maxillary and premaxillary teeth small, a palatal row paralleling the maxillary row.

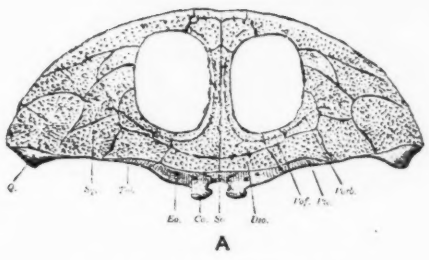

FIG. 136. *Plagiosternum*. Abel.

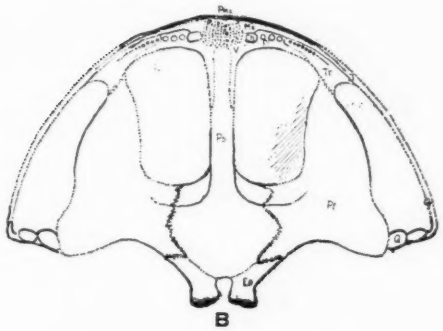

FIG. 137. *Plagiosuchus*. Huene.

12. Nares. External nares small, nearly terminal.
13. Lachrymal uncertain.
16. Otic notch absent.

Plagiosternum (fig. 135*A*, *B*, 136*A*) has the characters:

9. Skull as in *Plagiosaurus;* condyles posterior to edge of skull.
10. Orbits very large, near together.
11. Teeth. A palatal row paralleling the maxillary row.
12. Nares. External nares small, not terminal.
13. Lachrymal lateral to orbits, not touching the naris.
16. Otic notch absent.

Plagiosuchus (fig. 137*B*) is regarded by most as a member of the Brachyopidae but Huene (1922) places

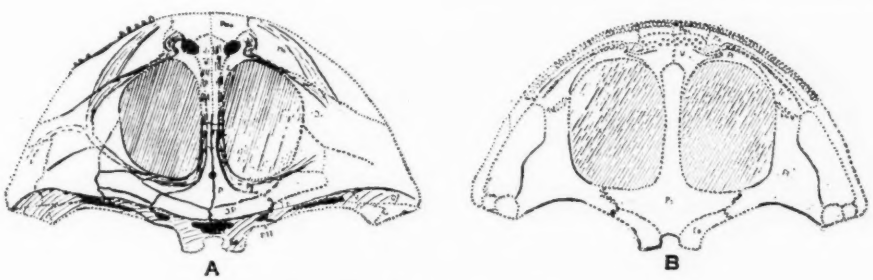

FIG. 135. *Plagiosternum*. Huene.

it in a distinct family, the Plagiosuchidae. The characters are:

9. Skull broader than long, occipital condyles far behind the articulation for the lower jaw; parasphenoid sutured to the pterygoids and occipitals, body and process broad; pterygoid does not reach prevomer; interpterygoid vacuities large, rectangular.
11. Maxillary teeth small; a palatal row paralleling the maxillary row.

Huene (1922) says that *Plagiosuchus* differs from *Batrachosuchus* only in the sculpture of high tubercles and but for this it should be put in the latter genus, but the restorations do not bear this out.

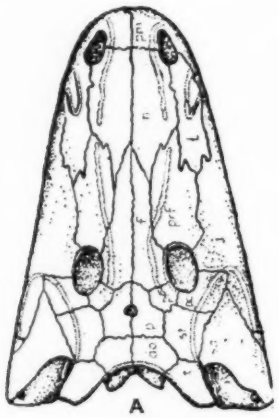

FIG. 138. *Capitosaurus*. Romer.

CAPITOSAURIDAE

This family is accepted by all. Its characters are:

9. Skull longer than broad, snout broad; frontal long and broad, taking part in the border of the orbit; parasphenoid slender; postorbital short.
10. Orbits small, far back, close together.
13. Lachrymal touching neither orbit nor naris.
14. Cornua absent, or small.
16. Otic notch medium.

Capitosaurus (fig. 138*A*, 139*B*) (*Parotosaurus*). The characters of *Capitosaurus* are:

9. Skull elongate in the antorbital region, snout broad; nasals equaling or exceeding frontals in length; anterior end of parasphenoid process narrow, ending between prevomers; anterior palatal vacuity single.
10. Orbits small, midlength of skull or in posterior half.
11. Teeth with palatal row paralleling the maxillary row; tusks on palatines and prevomers.

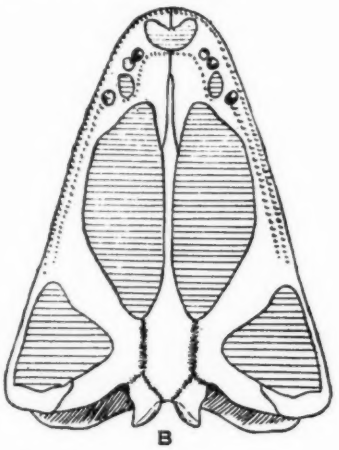

FIG. 139. *Capitosaurus*. Watson.

12. Nares. External nares elongate, oval, separated, not terminal.
13. Lachrymal touches neither orbit nor naris.
14. Cornua small.
16. Otic notch deep, open.

Kestrosaurus (fig. 140*A*, *B*) is accepted by all. The characters are:

9. Skull more elongate than *Capitosaurus;* anterior palatal vacuities double; anterior wing of the pterygoid rugose; basioccipital present "as a rough circular ossification on dorsal surface of the parasphenoid"; basisphenoid ? present, the ossification mentioned above may be the basisphenoid; an interfrontal present.
11. Teeth. A palatal row paralleling the maxillary row; tusks on the palatines and prevomers.
12. Nares. External nares small, round, wholly on the upper surface. Internal nares larger, oval, lateral.

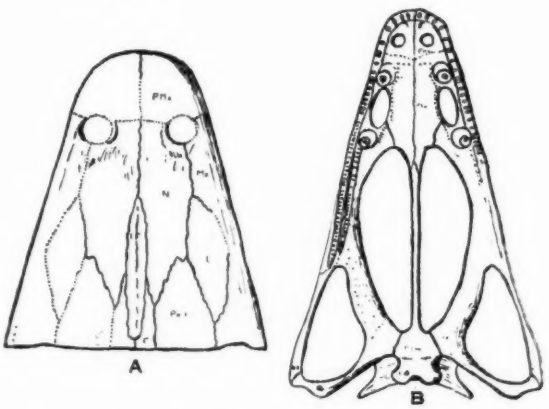

FIG. 140. *Kestrosaurus*. Haughton.

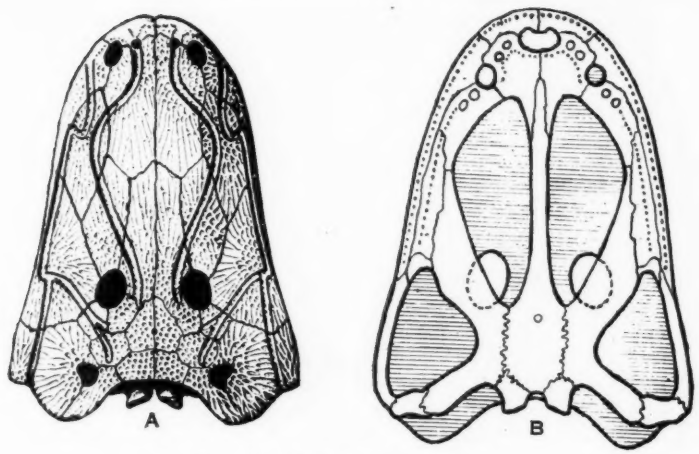

FIG. 141. *Cyclotosaurus*. Bystrow.

13. Lachrymal touches neither orbit nor naris.
16. Otic notch medium size.

Cyclotosaurus (fig. 141*A*, *B*) has the characters of *Capitosaurus* except:

16. Otic notch closed by junction of the tabular and squamosal.

Swinton (1927) describing a new species, *semiclausus*, from Cappel, Baden, Germany, discusses it as intermediate between *Capitosaurus* and *Cyclotosaurus*. Säve-Söderberg (1935) says that *Cyclotosaurus* has the postorbital meeting the lachrymal and excluding the jugal from the orbit.

MASTODONSAURIDAE

This family is accepted by all. The characters are:

9. Skull low, longer than broad, triangular; elongate in the preorbital region; frontals long and slender, take part in the border of the orbit; parasphenoid slender; palatal region anterior to the interpterygoid vacuities short; prevomer broad; post- and prefrontals broad and short; premaxillaries perforated for mandibular teeth (*Heptosaurus*).
10. Orbits large, in midlength of skull or a little posterior, close together.
11. Teeth. A palatal row paralleling the maxillary row; tusks on prevomer and palatine.
13. Lachrymal touching neither orbit nor naris.
14. Cornua triangular.
16. Otic notch pronounced.

Mastodonsaurus (fig. 142*A*, *B*). *Labyrinthodon* and *Salamandroides* are synonyms of *Mastodonsaurus*. The characters of the genus are those of the family.

Heptasaurus (fig. 143*A*), for *Mastodonsaurus cappelensis*, was placed in the Capitosauridae by Säve-Söderberg, but in the Mastodonsauridae by Kuhn.

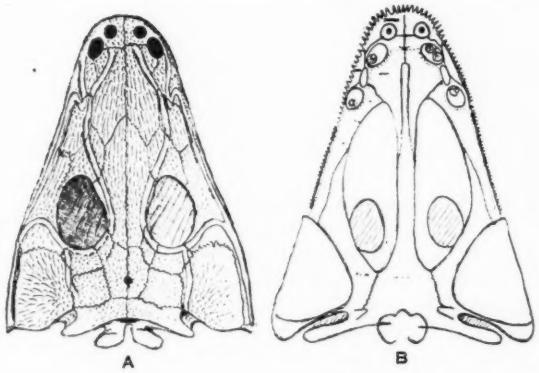

FIG. 142. *Mastodonsaurus*. Säve-Söderberg.

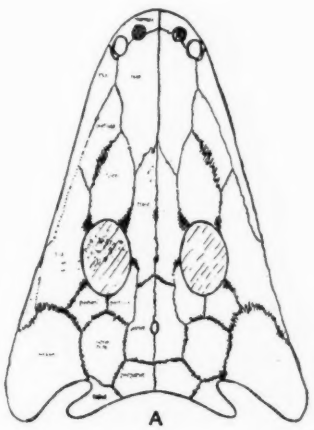

FIG. 143. *Heptasaurus*. Säve-Söderberg.

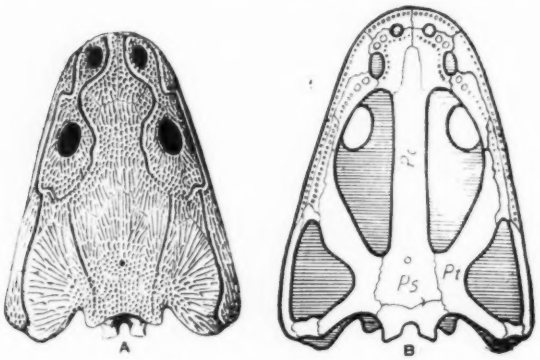

FIG. 144. *Metoposaurus*. Bystrow.

The characters distinguishing it from *Mastodonsaurus*, as given by Säve-Söderberg, are:

9. Skull. Postfrontal clearly present; preorbital portion longer; dermosupraoccipitals longer; tabular very broad, occasionally fenestrae for the mandibular teeth in the premaxillaries.
10. Orbits smaller, nearer midlength of the skull than in *Mastodonsaurus*, larger than in *Capitosaurus*.
12. Nares. External nares medium size, widely separated.
13. Lachrymal touching neither orbit nor naris.
14. Cornua present.
16. Otic notch deeper than in *Mastodonsaurus*.

The genus differs from *Capitosaurus* mainly in the larger orbits and the presence of fenestrae for the mandibular teeth.

METOPOSAURIDAE

This family is accepted by all. The characters are:

9. Skull low, broad, elongate; postorbital region elongated and broadened; postfrontal meets prefrontal excluding frontal from the orbit; process of the parasphenoid broad.
10. Orbits small to medium, in anterior half of the skull or near midlength, generally very anterior.
11. Teeth. Tusks on palatines and prevomers. A palatal row paralleling the maxillary row.
12. Nares. External nares large; "somewhat larger than the orbits" (Säve-Söderberg 1935).
13. Lachrymal touching neither orbit nor naris.
14. Cornua slight or absent.
16. Otic notch slight.

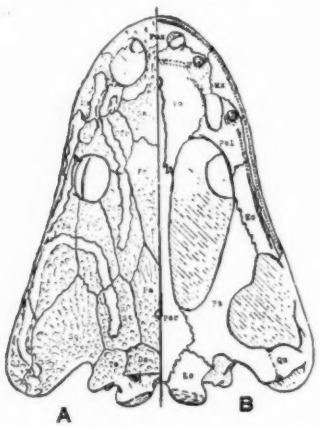

FIG. 145. *Koiskinodon*. Branson and Mehl.

Metoposaurus (fig. 144*A*, *B*) (for *Metopias* preoccupied). The characters are those of the family.

Koiskinodon (fig. 145*A*, *B*). The characters are:

9. Skull large; sensory canals well marked; anterior palatal vacuities round, paired, "exceptionally large" (Branson and Mehl); basioccipital cartilaginous or partly ossified, "probably visible to a slight degree in some specimens" (Branson and Mehl).
10. Orbits in anterior half of the skull but near midlength.

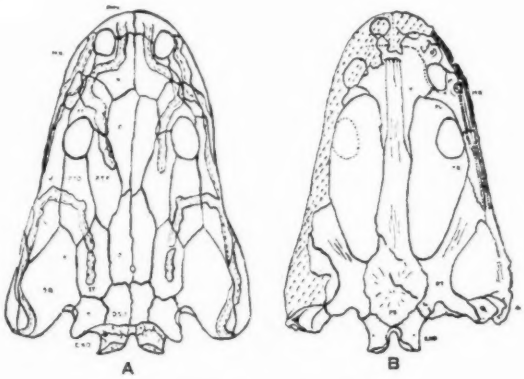

FIG. 146. *Buettneria*. Case.

11. Teeth with palatal row paralleling the maxillary row; tusks on prevomer and palatine.
12. Nares. External nares large, near anterior end. Internal nares more posterior, oval.
13. Lachrymal short, bordering orbit but not reaching naris.
14. Cornua small, formed by tabular.
16. Otic notch moderate size.

Kalamoiketor has much the same characters as *Koiskinodon* but differs in:

9. Skull. Bones very thin; the tabular one-half the size of the dermosupraoccipital.

Buettneria (fig. 146*A*, *B*) resembles closely the other Triassic Stereospondyls of North America. The characters are:

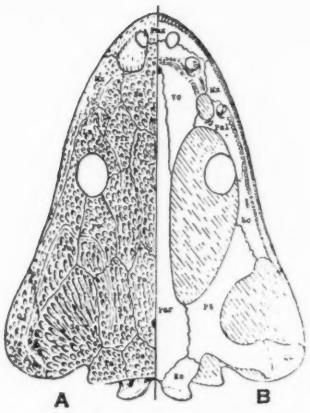

FIG. 147. *Borophagus*. Branson and Mehl.

9. Skull very flat; process of parasphenoid broad, body small; parasphenoid extends far forward between the prevomers; postorbital region elongated; sensory canal system well developed; postfrontal and postorbital long; anterior palatal vacuities small, anterior.
10. Orbits moderate size, oval, well forward, widely separated.
11. Teeth. A palatal row paralleling the maxillary row; tusks on palatine and prevomer.
12. Nares. External nares moderate size, separated. Internal nares larger, more posterior, widely separated.
13. Lachrymal touches neither orbit nor naris.
14. Cornua short.
16. Otic notch moderate size.

Borophagus (fig. 147*A*, *B*) has the characters:

9. Skull small, bones thin; snout sharper than in *Anaschisma;* parasphenoid process extends between prevomers; anterior palatal vacuities small, separated.

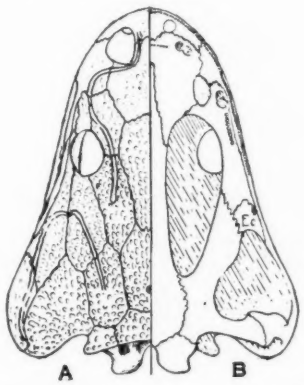

FIG. 149. *Anaschisma*. Branson and Mehl.

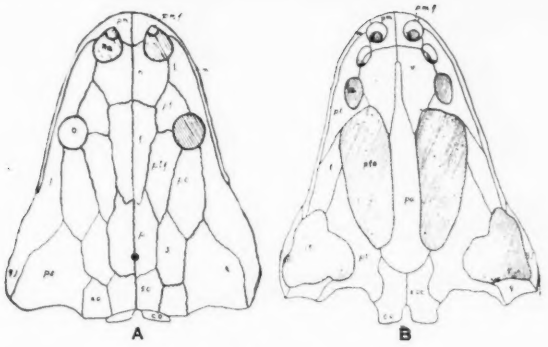

FIG. 148. *Anaschisma*. Branson.

10. Orbits small, in anterior half, separated.
11. Teeth. A palatal row paralleling the maxillary row; tusks on prevomer and palatine.
12. Nares. External nares large, anterior. Internal nares more posterior, oval.
13. Lachrymal touches neither orbit nor naris.
14. Cornua small.
16. Otic notch small.

Branson and Mehl regard *Borophagus* as the equivalent in Wyoming of *Kalamoiketor* in Arizona.

Anaschisma (fig. 148*A*, *B*, 149*A*, B) has the following characters:

9. Skull subtriangular, very flat anterior to the pineal foramen, more elevated posteriorly; premaxillaries relatively more elongated than in *Metoposaurus;* two pairs of anterior palatal vacuities.
10. Orbits subcircular, not oval.
11. Teeth. A palatal row paralleling the maxillary; tusks on prevomer and palatine.
12. Nares. External nares angularly oval, large. Internal nares larger, more posterior, widely separated.
13. Lachrymal short, touching orbit but not naris.
14. Cornua very small.
16. Otic notch slight or absent.

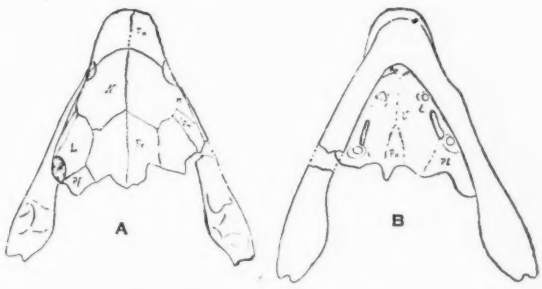

FIG. 150. *Rhytidosteus*. Huene.

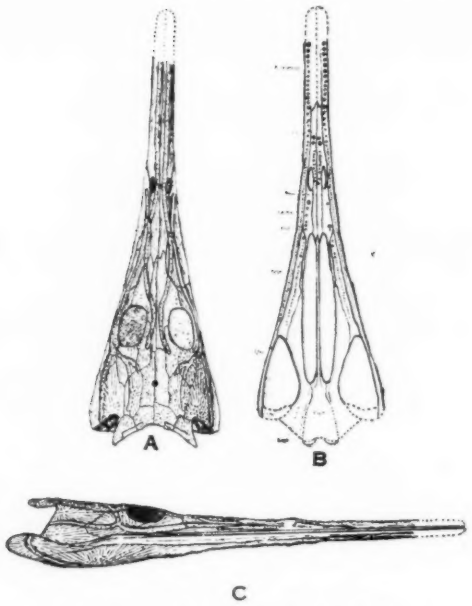

FIG. 151. *Aphanerama*. Säve-Söderberg.

RHYTIDOSTIDAE

This family is accepted by all. The characters are those of the single genus.

Rhytidosteus (fig. 150*A*, *B*) has only the anterior half of the skull and the lower jaws preserved. The characters are:

9. Skull depressed, long and triangular (broad, Huene 1920); interpterygoid vacuities short and broad; vomerine region relatively long.
10. Orbits medium size, lateral and laterally directed; in posterior third of the skull.
11. Teeth as in *Capitosaurus*.
12. Nares. External nares one-fourth of skull length from one anterior end, lateral and laterally directed. Internal nares elongate, narrow.

TREMATOSAURIDAE

This family as now understood contains numerous genera from widely separated localities. The characters are:

9. Skull elevated; snout elongate, slender; palatal region elongate anterior to the interpterygoid vacuities; elongate in prenarial and preorbital regions: process of parasphenoid very high and narrow, body of parasphenoid far back; anterior palatal vacuities large; septomaxillary present.
10. Orbits large or of medium size, lateral; near midlength of skull.
11. Teeth. Tusks on prevomer and palatine. A palatal row paralleling the maxillary row.
12. Nares. External nares small, near anterior end.
13. Lachrymal touches neither orbit nor naris.
14. Cornua short.
16. Otic notch well developed.

Aphanerama (fig. 151*A*, *B*, *C*). Efremov (1937) considers *Lonchorhynchus* as a synonym of *Aphanerama*, and Huene's ? *Aphanerama kannemeyeri* of South Africa is in all probability a synonym of *Trematosaurus*. The characters are:

9. Skull high, elongate, snout narrow; process of parasphenoid very narrow, body extends far back; parietal large, tapers anteriorly to anterior edge of the orbit; a centro-parietal bone, median unpaired, posterior to the parietal; frontal long and narrow, sensory canal system well developed.
10. Orbits small or medium size, lateral. Large in posterior half of the skull, widely separated (Smith-Woodward).
11. Teeth. A palatal row paralleling the maxillary row; denticles on the pterygoid.
12. Nares. External nares far back, near midlength of the skull.
14. Cornua small.
16. Otic notch well marked.

Gonioglyptus (fig. 152*A*, *B*) occurs in the Prionolobus Limestone with a salt water invertebrate fauna as do Wiman's Stegocephalians from Spitzbergen. Most writers put this genus in the Trematosauridae, Watson in the Stereospondyli, probably indeterminate. The characters are:

9. Skull sharp anteriorly; preserved portion permits assumption that there was a long, slender

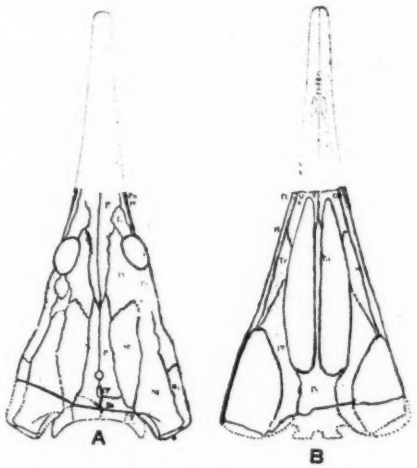

FIG. 152. *Gonioglyptus*. Huene.

snout; interpterygoid vacuities long, large, accuminate anteriorly; a centro-parietal as in *Aphanerama*.

10. Orbits oval, oblique, lateral; probably near midlength of skull.
11. Teeth. A palatal row paralleling the maxillary row; tusk on palatine, denticles on pterygoid, parasphenoid, and ectopterygoid.
13. Lachrymal small, short, touches orbit but not naris.
15. Intertemporal present (this is unique and amazing if true).
16. Otic notch rather deep and narrow.

Lonchorhynchus (fig. 153*A*, *B*) is accepted by all but Efremov, who (1937) considered it a synonym of *Aphanerama*. The characters are:

9. Skull elongate (Bystrow says longer than restored by Wiman); sensory canal system well developed.

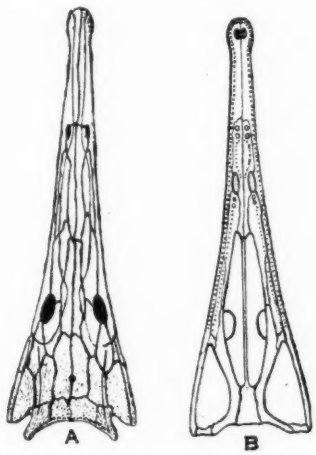

FIG. 153. *Lonchorhynchus*. Bystrow.

10. Orbits large, oval, well back.
11. Teeth. A palatal row paralleling the maxillary row; tusks on prevomer and palatine.
12. Nares. External nares far back, near middle of preorbital region (anterior end of the specimen not recovered).
13. Lachrymal uncertain.
14. Cornua short (Wiman) or more elongate (Bystrow).
16. Otic notch well developed.

Lyrocephalus (fig. 154*A*, *B*, *C*) is put in the Trematosauridae by all despite the notably different shape of the skull. The characters are:

9. Skull elongate, triangular; snout not long; anterior palatal vacuity large, single (as restored); septomaxillary present; a slit-like intermaxillary vacuity (Efremov 1935).

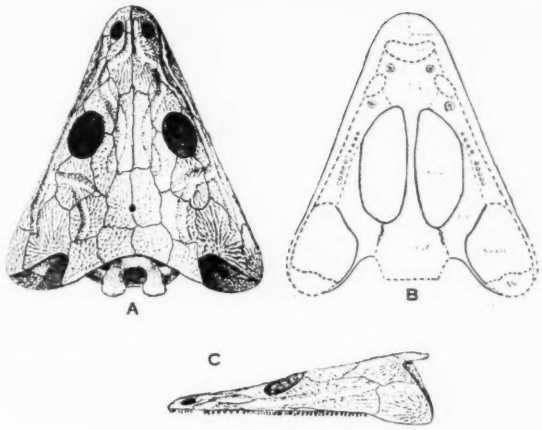

FIG. 154. *Lyrocephalus*. Säve-Söderberg.

10. Orbits moderate size, near midlength of skull, oval, separated.
11. Teeth. A palatal row paralleling the maxillary row; tusks on palatine, prevomer and ? ectopterygoid; denticles on parasphenoid and pterygoid.
12. Nares. External nares moderate size; far forward.
13. Lachrymal small, touching neither orbit nor naris.
14. Cornua tabular, small.
16. Otic notch well developed.

Microposaurus (fig. 155*A*, *B*) has the characters:

9. Skull triangular, more elongate than *Lyrocephalus;* anterior palatal vacuities small, paired; articulation for the lower jaw posterior to occipital condyles.
10. Orbits small, lateral, in anterior half of the skull.

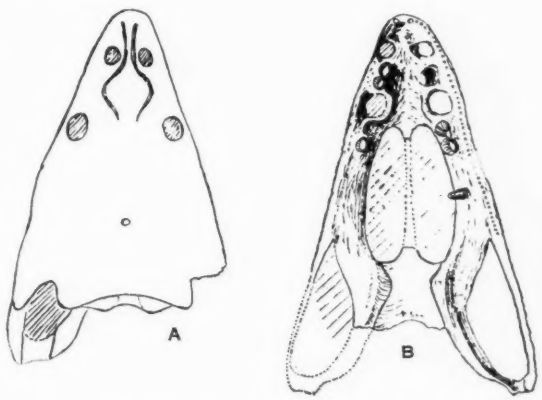

FIG. 155. *Microposaurus*. Haughton.

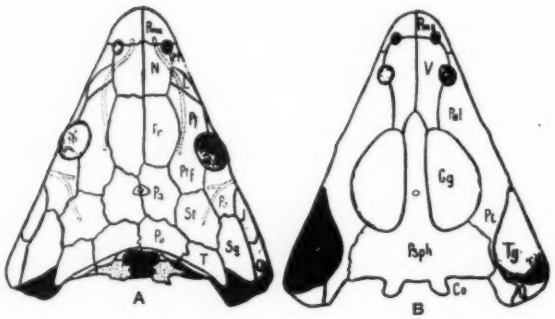

FIG. 156. *Peltostega*. Wiman.

11. Teeth. Palatal row not evident in specimen; tusks on prevomers, palatines, and ectopterygoids; denticles on pterygoid.
12. Nares. External nares anterior not terminal. Internal nares large, round, well back, separated.
13. Lachrymal uncertain.
14. Cornua short.
16. Orbit notch small.

Peltostega (fig. 156*A*, *B*) (*Peltostegus*) is put in the Trematosauridae (Kuhn), the ? Metoposauridae (Smith-Woodward), and a distinct family, Peltostegidae (Säve-Söderberg). The characters of the genus and the family Peltostegidae are:

9. Skull not elongate, more sharply triangular than *Lyrocephalus;* anterior palatal vacuities small, separated; prevomer long; body of parasphenoid very broad.
10. Orbits moderate size, midlength of skull, round, lateral.
12. Nares. External nares separated, not terminal. Internal nares more posterior, separated.
14. Cornua not large.
16. Otic notch moderate size.

Platystega (fig. 157*A*, *B*, *C*) is put in a subfamily Trematosaurinae (Säve-Söderberg) but in the Trematosauridae by others. The characters of the ? subfamily and the genus are:

9. Skull elongate, narrowed abruptly between orbit and nares; low anterior to the orbits; septomaxillary present; pineal foramen transversely oval; anterior palatal vacuities oval, paired; process of parasphenoid thin; interpterygoid vacuities large.
10. Orbits small, oval, lateral, looking partly lateral; a little posterior to midlength of skull.
11. Teeth with a palatal row paralleling the maxillary row; tusks on palatine and prevomer; denticles on pterygoid.
12. Nares. External nares moderate size, oval, not terminal. Internal nares well back, broadly oval.
13. Lachrymal touches neither orbit nor naris.
14. Cornua uncertain, posterior portion of skull incomplete.
16. Otic notch uncertain,

Stoschiosaurus (fig. 158*A*, *B*) is placed in the subfamily Trematosaurinae by Säve-Söderberg, but by others in the Trematosauridae. The characters are:

9. Skull probably, from the length of the frontal, elongate; posterior portion relatively broad; postorbital portion elongate.
10. Orbits large, lateral and looking partly lateral; probably anterior to the midlength of the skull.
16. Otic notch moderate size.

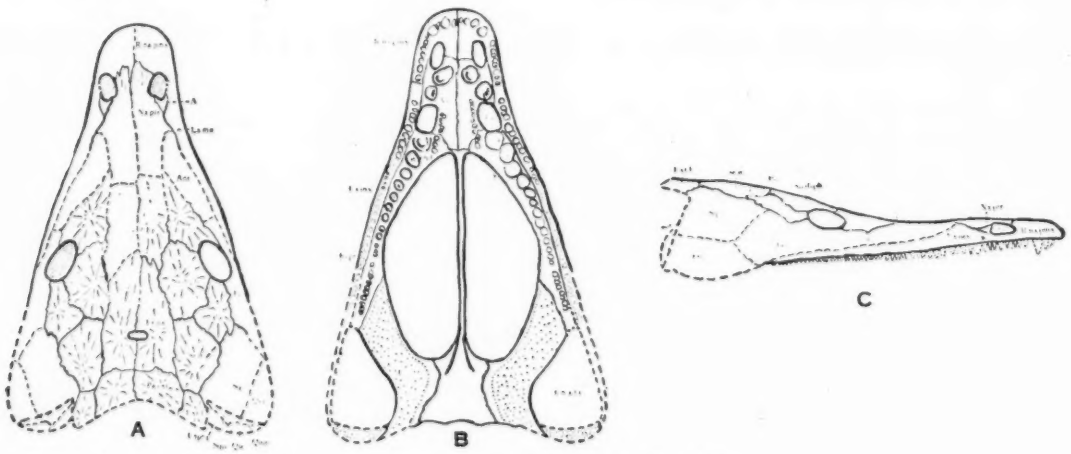

FIG. 157. *Platystega*. Säve-Söderberg.

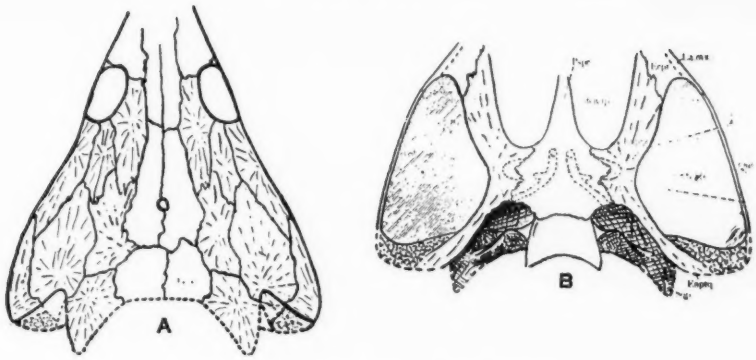

FIG. 158. *Stoschiosaurus*. Säve-Söderberg.

Tertrema (fig. 159*A*) has the characters:

9. Skull fairly high posteriorly, snout narrow; dermosupraoccipital very broad and short; anterior palatal vacuities long, oval, separate; a prominence between anterior palatal vacuities called ethmoid by Säve-Söderberg, but Wiman says it may be due to an injury.
10. Orbits small, midlength of the skull; widely separated, not so lateral as in *Stoschiosaurus*.
11. Teeth. A palatal row paralleling the maxillary row; tusks on palatines, prevomers, and ectopterygoids.
12. Nares. External nares elongate oval, well back. Internal nares elongate oval.

Thoösuchus (fig. 160*A*, *B*) (for *Lyrocephalus acutirostris*) is placed in the Benthosuchidae (Säve-Söderberg), Trematosauridae (Hartmann-Weinberg and Kuzmin). The characters are:

9. Skull elongate, triangular, snout not drawn out; anterior palatal vacuities round, separated by a broad bony septum; nasal region longer and narrower than in *Benthosuchus;* parasphenoid process long and narrow; ectopterygoid rod-like; sensory grooves well developed.
10. Orbits somewhat posterior to midlength of skull.
11. Teeth. A palatal row paralleling the maxillary row; tusks on palatines, prevomers, and ectopterygoids.
12. Nares. Internal nares well back, elongate oval.
13. Lachrymal touching orbit but not naris.
14. Cornua small.
16. Otic notch well developed.

Efremov (1940) regarded *Thoösuchus* as an "evolutionary derivitive" from *Benthosuchus* toward a more agile, carnivorous habit. He puts *Benthosuchus*, *Wetlugasaurus*, and *Capitosaurus* in a series beginning in Lower Permian with *Eryops* and enduring to Upper Triassic with *Cyclotosaurus*.

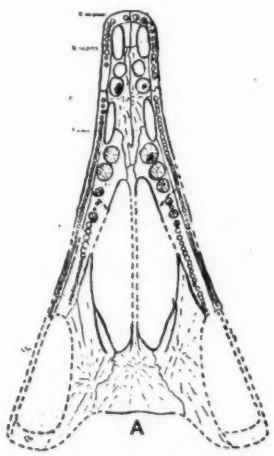

FIG. 159. *Tertrema*. Säve-Söderberg.

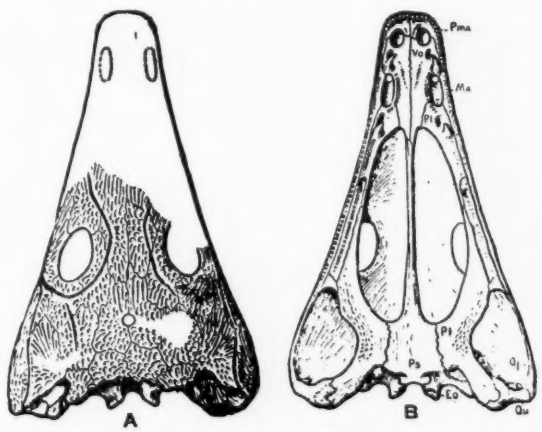

FIG. 160. *Thoösuchus*. Efremov.

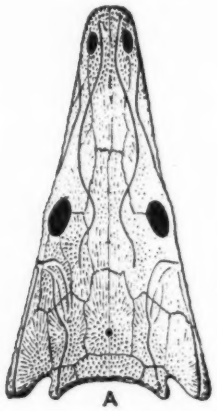

FIG. 161. *Trematosaurus*. Bystrow.

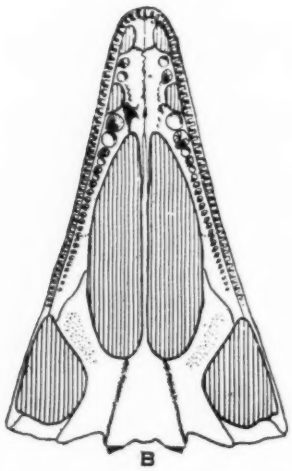

FIG. 162. *Trematosaurus*. Watson.

Trematosaurus (fig. 161*A*, 162*B*, 163*A*) has the characters:

9. Skull elongate; basioccipital and basisphenoid absent; fenestrae at anterior end of snout for mandibular teeth; anterior palatal vacuities separated by a broad septum; an interfrontal present.
10. Orbits oval, midlength of the skull.
11. Teeth. A palatal row paralleling the maxillary row; tusks on prevomer and palatine; denticles on pterygoid.
12. Nares. External nares separate, nearly terminal.
14. Cornua moderate size.
16. Otic notch moderate size.

Trematosuchus (fig. 164*A*, *B*) (for *Trematosaurus sobeyi*) has the characters of Trematosaurus, except:

9. Skull has no perforations of snout for the mandibular teeth; no anterior palatal vacuities (Haughton says present); small slit between premaxillaries may be remnant of intermaxillary vacuity; interfrontal present.
11. Teeth. Palatine and ectopterygoid teeth different. Tusks on prevomers, palatines, and ectopterygoids (Haughton); no palatal row paralleling the maxillary row.

Haughton accepts Watson's ideas in part but says that on reexamination the differences "fall away" and the two genera are "closely allied."

WETLUGASAURIDAE

This family, with the single genus *Wetlugasaurus*, is of very dubious standing. It was erected by Säve-Söderberg (1935) as a member of his Suborder Capito-

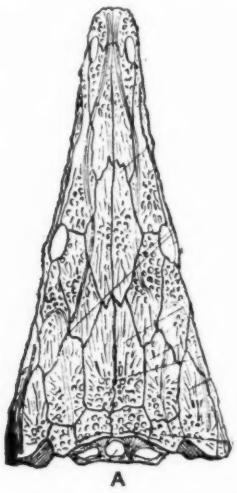

FIG. 163. *Trematosaurus*. Jaekel.

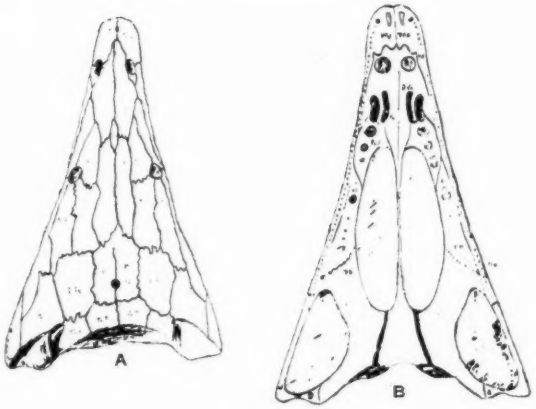

FIG. 164. *Trematosuchus*. Haughton.

sauroidei, with the following characters distinguishing it from the Capitosaurids.

9. Skull. Prefrontal meeting postfrontal (not so in any other Capitosaurid, Säve-Söderberg, 1935); postorbital about as broad as long; supratemporal markedly longer than broad; dermosupraoccipital about as long as broad; resembles *Capitosaurus* in the angular suture between the jugal and postorbital and the course of the vertical portion of the suborbital sensory canal. The skull is typically Capitosaurid, but with primitive characters such as the meeting of the prefrontal and postfrontal, but the vertebrae are rhachitomous. Säve-Söderberg said (1935) that the genus is "hardly to be separated from the Capitosauridae. However it may for the present be placed in a new family of its own—the Wetlugasauridae," and (1935) he refers to it as the "rhachitomous Capitosauroid, *Wetlugasaurus*." It is apparently in the stage of the Neorhachitomi of Efremov.

Bystrow and Efremov (1940) assert that the separation of *Wetlugasaurus* from *Benthosuchus* is not justified.

Wetlugasaurus (fig. 165*A*, *B*) has been placed in the Rhinesuchidae (Smith-Woodward, Kuhn), Benthosuchidae (Bystrow and Efremov), Wetlugasauridae, Stereospondyli (Säve-Söderberg), and intermediate between Rhachitomi and Stereospondyli (Efremov).

The characters as given by Riabinin are:

9. Skull narrower and longer than in *Rhinesuchus;* posterior portion elevated; sharp depression anterior to orbits.
10. Orbits oval, in posterior half of the skull; a depression between orbits.
11. Teeth. A palatal row paralleling the maxillary row; tusks on prevomers and palatines; denticles on prevomers, palatines, pterygoids, and ectopterygoids.
14. Cornua long.
16. Otic notch deep.

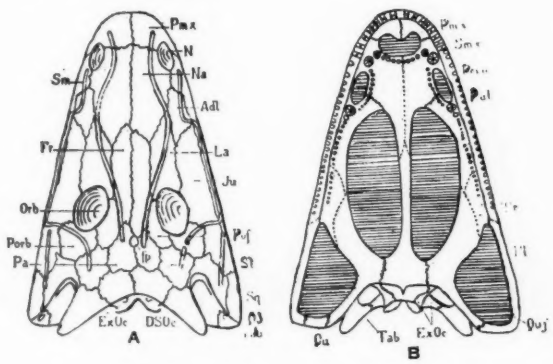

FIG. 165. *Wetlugasaurus*. Riabinin.

Bystrow and Efremov (1940) said that of all the Labyrinthodonts *Benthosuchus* most closely resembles *Wetlugasaurus*. *Wetlugasaurus* differs from *Benthosuchus* in:

1. "Somewhat" different sculpture.
2. Wider snout; very large, round, single fenestra premaxillaris (? anterior palatal vacuity).
3. Teeth on the prevomer in a wide arc posterior to the anterior palatal vacuities.
4. Process of parasphenoid "slightly" more massive.
5. Occiput comparatively narrow and high.
6. "Somewhat" less degree of reduction of the cartilaginous elements of the neurocranium.
7. "Somewhat" greater ossification (an earlier stage) of the post-cranial skeleton, sphenethmoid and epipterygoid.

They said *Wetlugasaurus* and *Benthosuchus* diverge only in adaptive characters in the same time interval. *Wetlugasaurus* is somewhat more primitive as shown by early stages of *Benthosuchus*, but both are in the same state of the vertebrae, which they call neorhachitomous. *Wetlugasaurus* more terrestrial but adapted to an aquatic life later than *Benthosuchus*. The "close genetic relationship of the two forms is beyond any doubt." Further they assert the division into two families not justified. *Benthosuchus*, *Wetlugasaurus*, and *Capitosaurus* are closely related genetically and to this group "probably" belongs *Mastodonsaurus*. *Benthosuchus* has the same type of variation from the Capitosaurids as has *Trematosaurus* and *Mastodonsaurus;* all are convergent adaptations in genetically different lines.

INDETERMINATE FORMS OF STEREOSPONDYLI

A considerable number of specimens have been described from inadequate material and many have been given names that subsequently proved to be synonyms.

Calamops, a half of a lower jaw from the Triassic of Pennsylvania, U.S.A. It has been placed in the Metoposauridae (Watson, Säve-Söderberg with doubt) *incertae sedis* (Camp *et al*).

Diadetognathus, a lower jaw from the Keuper of Warwickshire, England. Placed in the Mastodonsauridae (Watson, Smith-Woodward).

Dictyocephalus, the posterior half of a skull, from the Triassic of North Carolina, U.S.A. Placed in the Metoposauridae (Smith-Woodward, Kuhn), indeterminate (Watson, Säve-Söderberg).

Ekbainacanthus, fragments of the axial skeleton and one-half of a tooth, from the Middle Triassic of Spitzbergen. Stereospondyl (?) *incertae sedis* (Watson, Säve-Söderberg), reptile (Smith-Woodward, Kuhn).

Eupelor, portion of a skull, from the Triassic of Pennsylvania, U.S.A. *Incertae sedis* (Kuhn).

Gerrothorax, parts of the axial skeleton from the Rhaetic of Schonen, Bjuv, Sweden. Placed in the Brachyopidae (Nilson).

Glyptognathus, fragment of a lower jaw from the Panchet, Triassic of India. Placed in the Trematosauridae (Smith-Woodward, Kuhn), indeterminate, probably Stereospondyl (Watson), indeterminate (Säve-Söderberg).

Hercynosaurus, ribs, intercentra and tooth from Upper Keuper of Halberstadt, Germany. Placed in the Mastodonsauridae (Smith-Woodward, Kuhn).

Hyperokynodon, impression of a palate from the Schilfsandstein, Triassic of Heilbronn, Germany. Placed in the Mastodonsauridae (Kuhn), *incertae sedis* (Säve-Söderberg). Kuhn (1933) said that an account of this specimen would appear in the *Palaontologische Zeitschrift*, vol. 15, but the present author cannot find such a report.

Labyrinthodon, a synonym of *Mastodonsaurus*.

Mentosaurus, an incomplete lower jaw from the Triassic of Nietleben, near Halle, Germany. Placed in the Mastodonsauridae (Kuhn), perhaps a separate family (Kuhn), ? Mastodonsauridae (Smith-Woodward), indeterminate (Säve-Söderberg).

Odontosaurus, lower jaw and fragments of skull from the Upper Bunter sandstone of Sulzbad, Germany. Placed in the Mastodonsauridae (Kuhn), *incertae sedis* (Säve-Söderberg), not mentioned by others.

Pachygonia, fragments of a skull from the Panchet, Triassic, of India. Placed in the Mastodonsauridae (Smith-Woodward, Kuhn), probably a Stereospondyl (Watson), *incertae sedis* (Säve-Söderberg).

Pariostegus, fragments of a skull from the Triassic of North Carolina, U.S.A. Stereospondyl (Kuhn). Placed in the Temnospondyl (Smith-Woodward), *incertae sedis* by others.

Platyceps preoccupied, a synonym of *Bothriceps*, perhaps. A flattened skeleton of a small Labyrinthodont from the Hawksbury Shale, Triassic of New South Wales, Australia. An immature (larval) stage of *Bothriceps* ? (Smith-Woodward, Lydekker, Watson, Kuhn).

Ptychosphenodon, fragments of a lower jaw and teeth from the Upper Karroo of Aliwal North. Placed in the Mastodonsauridae (Smith-Woodward, Kuhn), probably a Stereospondyl (Watson), *incertae sedis* (Säve-Söderberg).

Rasaurus from the Lower Triassic of the Russian Platform. So far as the present writer can ascertain, a *nomen nudum*. Kuzman in 1937 and 1938 refers repeatedly to *Rasaurus* but gives no description or figure. The name does not appear in the *Zoological Record* or in *Biological Abstracts*.

Salamandroides, a synonym of *Mastodonsaurus*.

Stanocephalosaurus, the impression of the anterior half of a skull from the Middle Triassic of the vicinity of Winslow, Arizona, U.S.A. Placed in the Capitosauridae by Brown, but resembling certain Trematosaurids more closely.

Syphonodon, a single tooth from the Cynognathus Zone of Wanderboom, near Burghersdorf, South Africa. Placed in the Mastodonsuridae ? (Smith-Woodward), Mastodonsauridae (Kuhn), *incertae sedis* (Säve-Söderberg).

Trigonosternum, an interclavicle from the Lettenkohl of Kölleda, Thuringia. Placed in the Metoposauridae (Kuhn), indeterminate (Säve-Söderberg).

Xestorrhytias, a small fragment of a skull, perhaps the squamosal, from the Muschelkalk of Luneville, France. Placed in the Brachyopidae ? (Smith-Woodward), Brachyopidae (Kuhn), probably a Stereospondyl (Watson), perhaps a synonym of *Plagiosternum* (Smith-Woodward).

ADELOSPONDYLI

In 1929 Watson proposed the Order Adelospondyli with the description:

> The dorsal vertebra consists of a centrum, of uncertain character, which is rather accurately cylindrical in shape. The articular faces are conical pits which meet in the middle and communicate through a small persistent notochordal foramen. The upper surface of the centrum bears a pair of roughened depressions for the attachment of the neural arch. The cylindrical surface of the centrum is broken by a pair of deep pits which enter it symmetrically and are so placed that they and the mid-dorsal point divide the surface into three equal-sized parts. The pits extend inwardly nearly to the notochordal space. The centrum has an outer surface composed of a thin skin of dense bone but the greater part of its substance is composed of delicate bone strands or lamellae.
>
> The neural arch is single, and articulates with the centrum by coarsely jagged sutures. The pedicels of the arch are short, so that the posterior zygapophyses project far backward. The anterior zygapophyses rest immediately on the pedicels and their articular faces are directed upward and slightly inward. The neural spine is low and short and rises immediately above the postzygapophyses; the anterior border is split by a deep groove so that it appears double.
>
> There is a powerful transverse process which arises from the pedicel immediately below the anterior zygapophysis, and passes outward.

The Order is distinguished from the Lepospondyli and the living Amphibians by the typical sutural attachment of the neural arch to the centrum. Smith-Woodward added to Watson's description:

The ribs are long and curved, usually with a double head; the cranial roof over the temporal region tending to be reduced; occipital condyle double; parasphenoid very large and broad; jaws relatively short; branchial arches large and well ossified. He adds that in such respects as these forms diverge from the other Stegocephalia they approach the Urodela, of which they may have been the ancient forms. The recognition of the group Adelospondyli permitted the assemblage of several genera that had previously been referred to very diverse groups, even Classes. In the

XUM

Adelospondyli appears for the first time the wide, and at times seemingly lawless, departure from the typical number and arrangement of the roofing bones in the Stegocephalia, a departure that is evident in the Urodela and the Gymnophiona and has caused them to be derived from the Adelospondyli by various workers. Westoll (1943) says of the constituent genera, however: "They are so variable in cranial structure that the group may be heterogeneous" and ". . . there is no evidence to suggest that any member was independently derived from fishes." The diversity of opinion as to the content of the Adelospondyli is illustrated by the fact that in addition to the genera listed below, Steen (1938), Westoll (1943), and Watson (1940) have included *Hylonomus*, *Hyloplesion*, and *Miobrachis* in the group, in contrast with most workers who have classified these genera as Lepospondyli.

List Showing the Classification, Geological Horizon, and Location of the Determinable Adelospondyli

Adelogyrinidae
- *Adelogyrinus*, Lower Carboniferous, Mississippian, from near Edinburgh, Scotland.
- *Dolichopareias*, Lower Carboniferous, Mississippian, from near Edinburgh, and from Fifeshire, Scotland.

Lysorophidae
- *Lysorophus*, Middle Carboniferous, of Vermillion County, Illinois, U.S.A. Lower Permian, Clear Fork, of Texas, U.S.A.
- *Cocytinus*, Middle Carboniferous, Allegheny Formation, of Linton, Ohio, and Cannelton, Pennsylvania, U.S.A.

Family indeterminate
- *Gymnarthrus*, Lower Permian, Clear Fork, of Texas, U.S.A.
- ? *Pariotichus*, Lower Permian, Clear Fork, of Texas, U.S.A.
- ? *Cardiocephalus*, Lower Permian, Clear Fork, of Texas, U.S.A.

Adelogyrinidae

Adelogyrinus (fig. 166*A*, *C*) has the characters of the family and genus:

8. Scutes. "Elaborate ventral armor of slender, elongate, rhomboid ossicles."
9. Skull long, low, pear-shaped; dorsal surface semielliptical in cross-section; parietal very long; parietal foramen large, elongate, keyhole-shaped; two circumorbital bones absent, probably the pre- and postfrontals; tabular absent.
10. Orbits large, oval, anterior, largely lateral.
11. Maxillary teeth a single series present only in the anterior half of the short maxillary; small, cylindrical, closely set.
13. Nares. External nares small, terminal.
14. Cornua formed by squamosal as the tabular is absent; overhanging otic notch.
16. Otic notch wide.

Dolichopareias (fig. 167*A*, *C*, 168*A*) has the characters:

9. Skull long, narrow, dorsal surface nearly semicircular in cross-section, snout truncate; dermosupraoccipital small, nearly square, forming the posterior edge of the skull; pre- and postfrontal and tabular absent. Closely similar to *Adelogyrinus* and *Lysorophus* in the anterior position of the orbits and the short maxillary.
10. Orbits small, very anterior, face outward and upward.

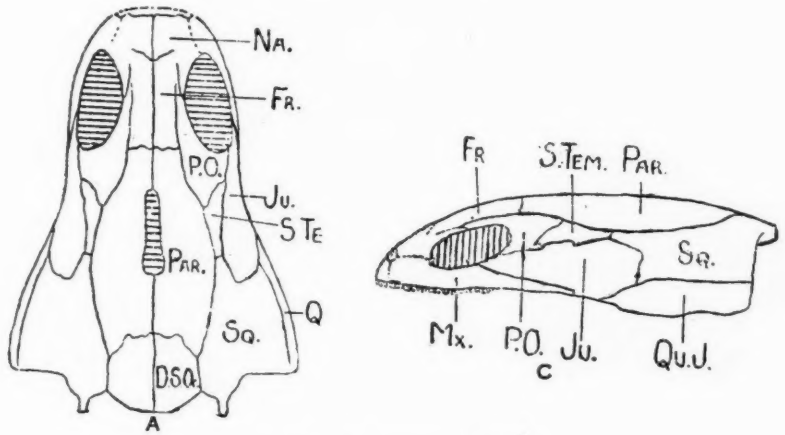

FIG. 166. *Adelogyrinus*. Watson.

Gerrothorax, parts of the axial skeleton from the Rhaetic of Schonen, Bjuv, Sweden. Placed in the Brachyopidae (Nilson).

Glyptognathus, fragment of a lower jaw from the Panchet, Triassic of India. Placed in the Trematosauridae (Smith-Woodward, Kuhn), indeterminate, probably Stereospondyl (Watson), indeterminate (Säve-Söderberg).

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The Order is distinguished from the Lepospondyli and the living Amphibians by the typical sutural attachment of the neural arch to the centrum. Smith-Woodward added to Watson's description:

The ribs are long and curved, usually with a double head; the cranial roof over the temporal region tending to be reduced; occipital condyle double; parasphenoid very large and broad; jaws relatively short; branchial arches large and well ossified. He adds that in such respects as these forms diverge from the other Stegocephalia they approach the Urodela, of which they may have been the ancient forms. The recognition of the group Adelospondyli permitted the assemblage of several genera that had previously been referred to very diverse groups, even Classes. In the

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Lysorophidae
- *Lysorophus*, Middle Carboniferous, of Vermillion County, Illinois, U.S.A. Lower Permian, Clear Fork, of Texas, U.S.A.
- *Cocytinus*, Middle Carboniferous, Allegheny Formation, of Linton, Ohio, and Cannelton, Pennsylvania, U.S.A.

Family indeterminate
- *Gymnarthrus*, Lower Permian, Clear Fork, of Texas, U.S.A.
- ? *Pariotichus*, Lower Permian, Clear Fork, of Texas, U.S.A.
- ? *Cardiocephalus*, Lower Permian, Clear Fork, of Texas, U.S.A.

Adelogyrinidae

Adelogyrinus (fig. 166*A*, *C*) has the characters of the family and genus:

8. Scutes. "Elaborate ventral armor of slender, elongate, rhomboid ossicles."
9. Skull long, low, pear-shaped; dorsal surface semielliptical in cross-section; parietal very long; parietal foramen large, elongate, keyhole-shaped; two circumorbital bones absent, probably the pre- and postfrontals; tabular absent.
10. Orbits large, oval, anterior, largely lateral.
11. Maxillary teeth a single series present only in the anterior half of the short maxillary; small, cylindrical, closely set.
13. Nares. External nares small, terminal.
14. Cornua formed by squamosal as the tabular is absent; overhanging otic notch.
16. Otic notch wide.

Dolichopareias (fig. 167*A*, *C*, 168*A*) has the characters:

9. Skull long, narrow, dorsal surface nearly semicircular in cross-section, snout truncate; dermosupraoccipital small, nearly square, forming the posterior edge of the skull; pre- and postfrontal and tabular absent. Closely similar to *Adelogyrinus* and *Lysorophus* in the anterior position of the orbits and the short maxillary.
10. Orbits small, very anterior, face outward and upward.

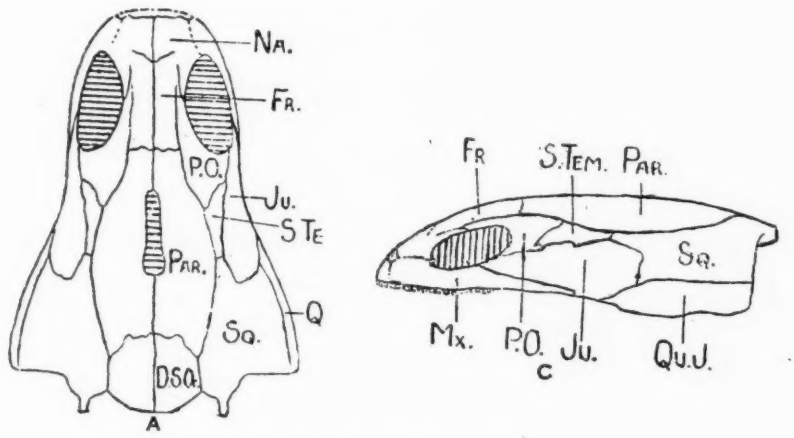
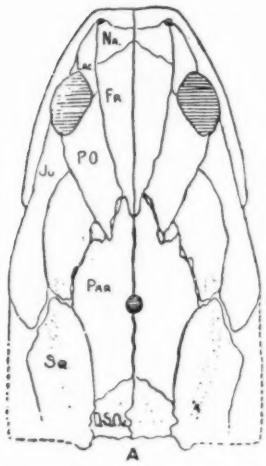


Fig. 166. *Adelogyrinus*. Watson.



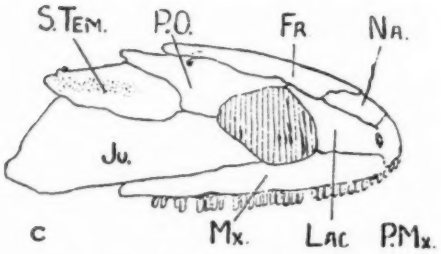


FIG. 167. *Dolichopareias*. Watson.

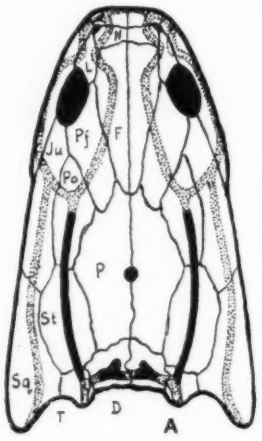


FIG. 168. *Dolichopareias*. Bystrow.

11. Teeth. Maxillary and premaxillary teeth small, isodont, cylindrical, closely set, with blunt points.
12. Nares. External nares small, nearly terminal.

LYSOROPHIDAE

Proposed by Williston to replace Paterosauridae (Broili), "which is not tenable." The characters are:

1. Body slender, *Amphiuma*-like.
3. Limbs ? absent or very small; feet unknown.
4. Girdles unknown.
5. Vertebrae notochordal, neural arches not united above; no chevrons.
6. Ribs long, single-headed.
8. Scutes absent.
9. Skull much elongated; postfrontal, lachrymal, jugal, quadratojugal, postorbital, and supratemporal absent; prefrontal articulating with nasal, frontal, and parietal; tabular present (absent in *Adelogyrinus*); basioccipital and basisphenoid present; pineal foramen much reduced or absent; parasphenoid large; occipital condyle single, concave.
10. Orbits confluent with open temporal region.
11. Teeth present on pterygoid and prevomer; teeth on jaws large, hollow cones.
12. Nares. External nares small, terminal.

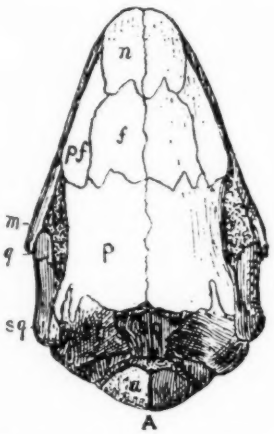


FIG. 169. *Lysorophus*. Williston.

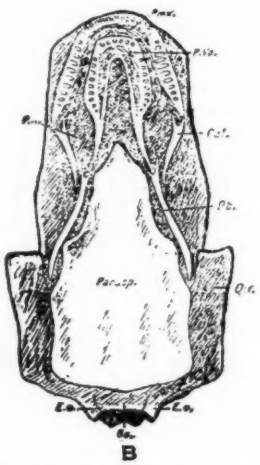


FIG. 170. *Lysorophus*. Broom.

13. Lachrymal absent.
14. Cornua absent.
15. Intertemporal absent.
16. Otic notch absent.

Lysorophus (fig. 169*A*, 170*B*, 171*C*) has been placed by many, if not most authors in the Urodela, but is now probably to be placed in the Adelospondyli. The characters are those of the family. (See difference of opinion of Kuhn, Broom, Huene, Sollas, who put it in or near the Urodela.)

Cocytinus (fig. 172*B*) with its probable synonyms, *Brachydectes* and *Pleuroptyx*, from Linton, Ohio, is accepted by all as close to *Lysorophus*. Certain specimens referred to *Molgophis* are regarded by Romer and Steen as belonging to *Cocytinus*. The characters are:

9. Skull much like that of *Lysorophus* (Romer, Steen), broad, flat; dorsal surface formed by nasals, frontals, parietals; supraoccipitals "must have appeared on the roof" (Steen); prefrontal articulates with nasal, frontal, and parietal; a minute parietal foramen (difference from *Lysorophus*, Steen).

Gymnarthrus (fig. 173*A*, *B*, *C*) was originally placed in the Reptilia, but was transferred to the Amphibia.

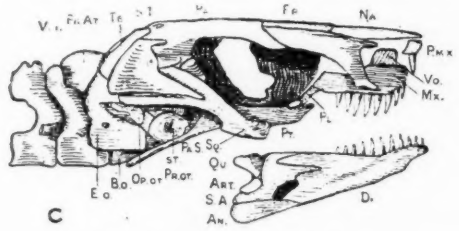


FIG. 171. *Lysorophus*. Sollas.

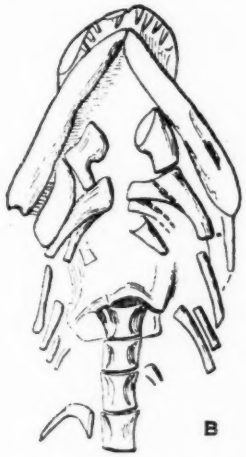
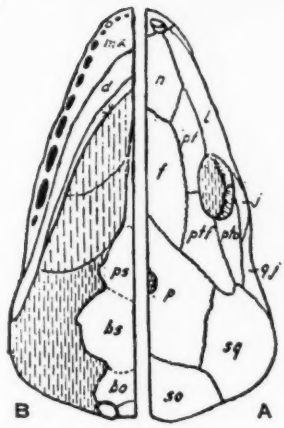


FIG. 172. *Cocytinus*. Romer.



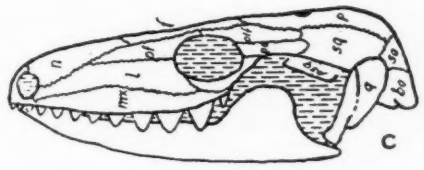


FIG. 173. *Gymnarthrus*. Case.

It is generally placed as indeterminate, near or in the Adelospondyli. Its characters are:

9. Skull elongate; postorbital, pre- and postfrontals, lachrymal present; supraoccipital on roof of skull; supratemporal present; squamosal small; parasphenoid (parasphenoid + basisphenoid) large posteriorly; process of parasphenoid small; basioccipital present; occipital condyle single; jugal ? absent; pineal foramen large; interpterygoid vacuities small.
10. Orbits oval, lateral, anterior to midlength of skull; closed posteriorly by the ? jugal.
11. Teeth blunt cones, increasing in size from before backward.
12. Nares. External nares moderate size, terminal.
13. Lachrymal extends from orbit to naris.
14. Cornua absent.
15. Intertemporal absent.
16. Otic notch absent.

Pariotichus (fig. 174*A*, *C*) generally thought to be a reptile, has been placed in the Adelospondyli, *incertae sedis*, by Romer. The characters are:

8. Skull elongate; temporal region covered; quadratojugal and tabular absent; parasphenoid, or parasphenoid + basisphenoid, long posteriorly; pineal foramen present.
10. Orbit large, round, lateral, in midlength of skull.

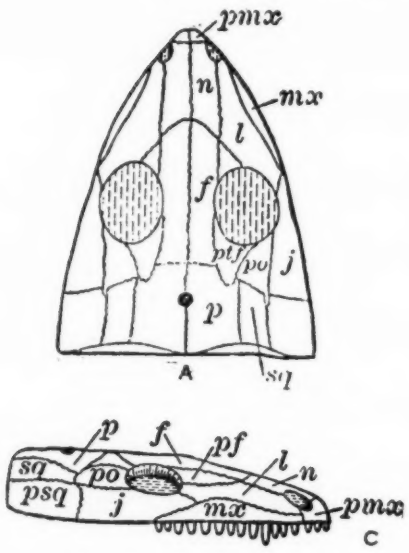


FIG. 174. *Pariotichus*. Case.

11. Teeth in jaws bluntly conical; decreasing in size from before backward.
13. Lachrymal extends from orbit to naris.
14. Cornua absent.
15. Intertemporal absent.
16. Otic notch absent.

Cardiocephalus (fig. 175*A*, *C*, 176*C*) (*Cardicephalus* in Hay) is close to *Gymnarthrus*. It has been regarded as a reptile. Bystrow considered it a synonym of *Gymnarthrus*. It probably belongs in the Adelospondyli. The characters are:

7. Sculpture absent, the bones "smooth and shining."
9. Skull pear-shaped; supratemporal and quadratojugal absent or minute; lyrae of the sensory canals present.

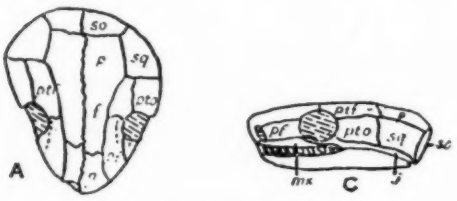


FIG. 175. *Cardiocephalus*. Case.

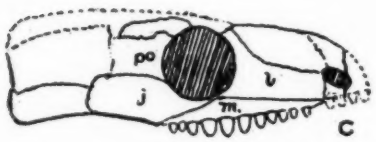


FIG. 176. *Cardiocephalus*. Williston.

10. Orbits large, lateral, in anterior half of the skull.
11. Teeth large, compressed with fore and aft cutting edges; reduced in size anteriorly.
12. Nares. External nares large, widely separated, terminal.
13. Lachrymal does not touch naris.
14. Cornua absent.
15. Intertemporal absent.
16. Otic notch absent.

ICHTHYOSTEGALIA

Watson's recognition in 1926 of the relationship of the Carboniferous Embolomeri to the Crossopterygian fish outlined the hiatus in the phylogenetic history of the Stegocephalia, which was so accurately filled by the discovery in the Devonian of Greenland of the Ichthyostegalia described by Säve-Söderberg in 1932. There has been no hesitancy in accepting the morphological significance of the group regardless of what taxonomic value be assigned to it, either as an Order equal in rank to the Stegocephalia or a lesser group within the Stegocephalia.

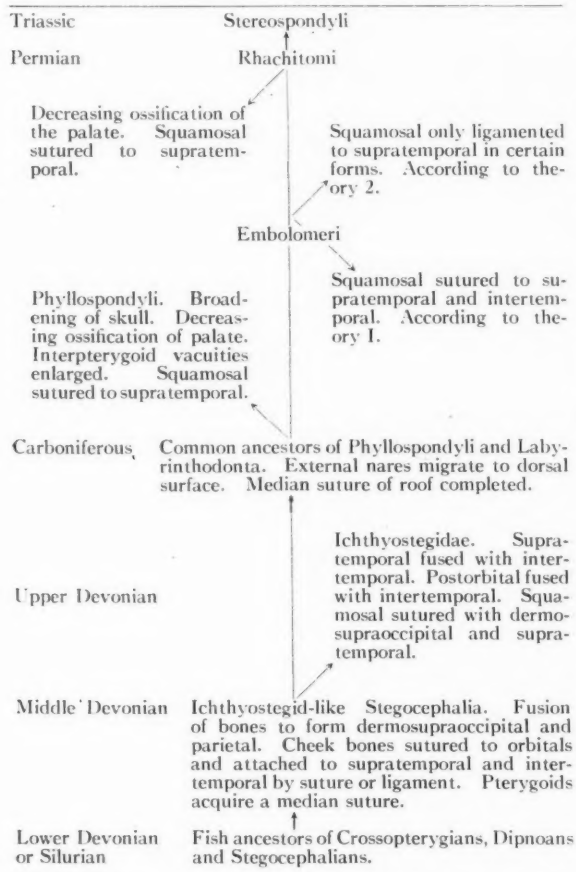
Säve-Söderberg in 1932 gave the following definition of the Ichthyostegalia:

Stegocephalians with external nares on the ventral side of the skull. Dermal cranial roof with an unpaired rostro-

SÄVE-SÖDERBERG'S TERMINOLOGY	TERMINOLOGY IN COMMON USE
Naso-rostro-premaxillary	Premaxillary
Naso-rostro-interrostro-premaxillary	
Interrostral	Internasal
Naso-postrostral	Nasal
Naso-postrostro-interrostral	
Median postrostral	Interfrontal
Frontal	Frontal
Anterior antorbital	Septomaxillary
Posterior antorbital	Lachrymal, Adlachrymal, Postnasal
Anterior supraorbital	Prefrontal, Lachrymal
Posterior supraorbital	Postfrontal
Supraorbito-dermosphenotic	
Dermosphenotic	Intertemporal
Fronto-parietal	Parietal
Parieto-extrascapular	Postparietal, Dermosupraoccipital
Median extrascapular	
Supratempero-intertemporal	Supratemporal, Squamosal, Suprasquamosal
Lateral extrascapular	Tabular
Lachrymo-maxillary	Maxillary
Jugal	Jugal
Postorbital	Postorbital
Postorbito-dermosphenotic	
Squamosal	Squamosal, Prosquamosal, Paraquadrate (Supratemporal)
Quadratojugal	Quadratojugal
Vomer	Prevomer, Vomer
Dermopalatine	Palatine
Ectopterygoid	Transverse, Ectopterygoid
Entopterygoid	Pterygoid
Parasphenoid	Parasphenoid

interrostral[13] and an unpaired parieto-extrascapular, a small anterior antorbital dorsally to each external naris, joined by a suture with the bones anterior, medial and posterior to it; at least in certain forms an independent preocular. Lateral line system of the head in greater part enclosed in the dermal bones; with a true jugal canal, possibly also with a quadratojugal canal. Palate extensively ossified, with very narrow interpterygoid vacuities, and with entopterygoids meeting in a median suture.

Though this order is as yet known only from the skull, there can be little doubt that the vertebrae and the postcranial skeleton must be of the same general type as those of the Embolomeri. Säve-Söderberg (1934) regarded the two groups as parallel developments from a common ancestor from which the Ichthyostegalia "have departed little." Because of the many characters inherited from the Crossopterygia, and because of suggestions from both their morphology and from the matrix in which the specimens are found, and from associated invertebrates, it is agreed that they are aquatic, though no immature forms showing gill structures have been found.


Triassic
Stereospondyli
Permian
Rhachitomi
Decreasing ossification of the palate. Squamosal sutured to supratemporal.
Squamosal only ligamented to supratemporal in certain forms. According to theory 2.
Embolomeri
Squamosal sutured to supratemporal and intertemporal. According to theory I.
Phyllospondyli. Broadening of skull. Decreasing ossification of palate. Interpterygoid vacuities enlarged. Squamosal sutured to supratemporal.
Carboniferous
Common ancestors of Phyllospondyli and Labyrinthodonta. External nares migrate to dorsal surface. Median suture of roof completed.
Ichthyostegidae. Supratemporal fused with intertemporal. Postorbital fused with intertemporal. Squamosal sutured with dermosupraoccipital and supratemporal.
Upper Devonian
Middle Devonian
Ichthyostegid-like Stegocephalia. Fusion of bones to form dermosupraoccipital and parietal. Cheek bones sutured to orbitals and attached to supratemporal and intertemporal by suture or ligament. Pterygoids acquire a median suture.
Lower Devonian or Silurian
Fish ancestors of Crossopterygians, Dipnoans and Stegocephalians.

[13] A table given by Säve-Söderberg showing the equivalents of his terminology with that in common use is repeated for convenience on page 410. A similar table showing the equivalents of the "orthodox" names for the skull bones of the Osteolepids and Stegocephalia with Säve-Söderberg's terminology was given by Westoll in 1943.

As is shown by the accompanying table modified from Säve-Söderberg (1932) he postulated a tetrapod form intermediate between the Ichthyostegalia and the fish. He came no nearer to indicating the ancestral form than to suggest the "fish ancestors of the Crossopterygians, Dipnoans and Stegocephalians."

In 1934, in his paper—"Some points of view concerning the evolution of the vertebrates and the classification of the group"—he made more definite suggestions in the form of seven points showing the relation between the Crossopterygians, Dipnoans, and Tetrapoda:

1. The lateral line system in all has a jugal canal and the ventral portion only, of the preopercular canal.
2. In all three groups the dermal bones of the dorsal surface are comparable.
3. The dermal bones of the cheek in the early Tetrapods and Crossopterygians are very similar. In the Dipnoans they are too much reduced for comparison.
4. The dermal bones of the lower jaw are comparable in all of them.
5. The presence of internal nares, as in the Crossopterygians (*Osteolepis* and *Dictyonosteus*), Dipnoans, and Tetrapods.
6. The sclerotic plates few in Elasmobranchs (generally 4) and Actinopterygians (2 or 4); many in Crossopterygians (11–28) and Tetrapods (Stegocephalia 20–32).
7. Limbs with a central axis in Crossopterygians, Dipnoans, and Tetrapods.

Upon the basis of these similarities he suggested a group, Choanata (1933), to include the Crossopterygians, Dipnoans, and Tetrapods, as distinct from the Elasmobranchs and Actinopterygians. The Choanata he divided into the Dipnoans leading to the Urodeles, and the Crossopterygia leading to a group, Eutetrapoda, which he further divided into the Batrachomorpha, which led through the Ichthyostegids to the Amphibia, and the Reptilomorpha, which led to reptiles, birds, and mammals. See arrangement following.

Vertebrate craniata
Branch Agnathi (Cyclostomata)
Branch Gnathostomata

I. Elasmobranchii

1. Acanthodi
2. Placodermi
3. Holocephala
4. Selachi

II. Choanata

A. 1. Dipnoi
2. Urodela
B. 1. Crossopterygii
2. Eutetrapoda
a. Batrachomorpha
Ichthyostegalia
Labyrinthodonta
Phyllospondyli
? Anura
b. Reptilomorpha
Anthracosauria
"Reptilia" (with exceptions)
Aves
Mammalia

III. Actinopterygia

In 1932 Säve-Söderberg listed as the important characters of the Ichthyostegids (fig. 177*A*, *B*, *C*):

1. The ventral position of the external nares.
2. The unpaired condition of the parietal and the rostral bones.
3. The presence, though reduced or vestigial, of a preopercular.
4. The enclosure in the roofing bones of the canals of the sensory system.

The Ichthyostegids share with the Embolomeri in the presence of large pterygoids (entopterygoids) meeting anteriorly in a suture and separated posteriorly by a vary narrow interpterygoid vacuity only partly divided by the small process of the parasphenoid. These characters are inherited from some Crossopterygian ancestor.

Westoll (1943) in a paper on the origin of the tetrapods has offered certain criticisms of Säve-Söderberg's interpretations of the specimens of Ichthyostegids, and of some of the conclusions and theories founded upon them. He states that cracks in the prefrontal bones have been mistaken for sutures and that cracks in the premaxillaries have been interpreted as a sensory canal groove. Further he states that comparison of Ichthyostegids with abnormal specimens of Osteolepids has led to a scheme of homologies involving differential fusion of bones which is not in accord with the facts. In greater detail he has pointed out that:

I. The posterior antorbital and the anteriorsupraorbital of Säve-Söderberg are in reality a single bone, a crack having been mistaken for a suture.

II. The tetrapod postparietal (dermosupraoccipital) is unpaired in the Ichthyostegids and the parietal may be partly so.

III. The dermosphenotic has no separate existence in the Osteolepid, *Elpistostege* (which Westoll regards as the nearest ancestor yet known of the tetrapods), or in the Ichthyostegids but is fused with the osteolepid intertemporal or postorbital. The intertemporal and supratemporal are fused in some Ichthyostegids and free in others.

IV. The bones of the snout have been misunderstood. The rostropremaxillaries are in reality a single bone, the supposed suture is a crack; the groove probably for the ethmoid commisure is a crack. The rostropremaxillary is a premaxillary the rostrointerrostral corresponds to the osteolepid postrostral, or Stegocephalian internasal. The snout and the sensory canals, as far as they are known, correspond exactly with those of the Rhipidistians and early Stegocephalians.

V. His restoration of the external nostril is different from that offered by Säve-Söderberg, being higher on the side, though still not free from the lower edge.

VI. The tetrapod frontals, nasals, interfrontals, and internasals occupy a space covered in the Osteolepids by the "nasals" and postrostrals. Westoll points out that this space was covered in primitive Dipnoi by a series of small elements, some along the course of the sensory canals and others more or less heterogeneously placed, and in the nature of anamestic (Wormian) bones. The origin from these of the tetrapod nasals

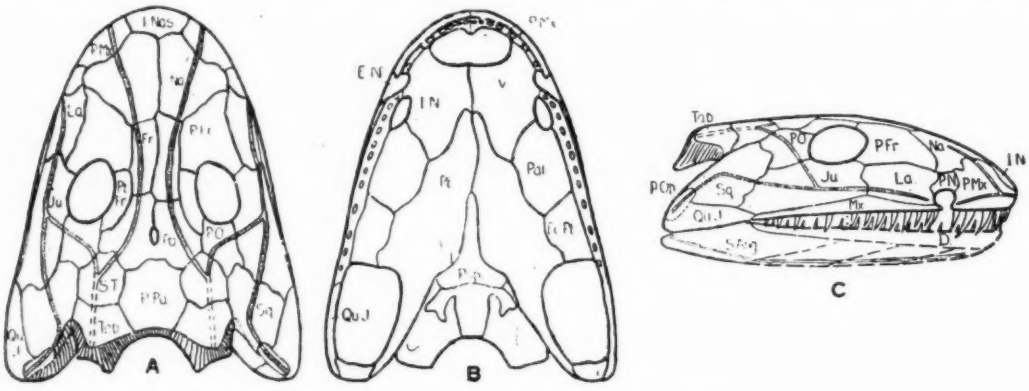


FIG. 177. An Ichthyostegid. Westoll

and frontals, and the fate of the postrostrals, is as yet not understood.

Westoll's conclusions are based on other considerations and characters than those of Stensio and Säve-Söderberg. Opposed to their dependence on the relations between the roofing bones of the skull and the sensory canals is his statement (1943), "It is therefore clear that there was no fundamental morphological connexion between the dermal bones and the latero-sensory system in Stegocephalia."

It is apparent that the same course is being taken with the Ichthyostegalia as with all other groups of the Stegocephalia; what was at first clear and well defined is being shown to be complicated and capable of most diverse interpretation.

ICHTHYOSTEGIDAE

(Säve-Söderberg, 1932)

Primitive labyrinthodont Stegocephalians of various size, with the dermal bones of the skull-roof and palate arranged in many respects like those of the Crossopterygians: with an unpaired parieto-extrascapular, an unpaired rostro-interrostral, premaxillaries wholly on the ventral side of the skull, fused with the lateral rostrals to compound rostro-premaxillaries, narrow frontals, and (probably always) small preopercular; with broad naso-postrostrals, large oblong posterior antorbitals and a small square anterior antorbital on each side between the rostro-premaxillary and the lachrymal; with large jugals, short fronto-parietals, and compound postorbito-dermosphenotics and supra-temporo-intertemporals. Squamosals rigidly connected by suture with the supratemporo-intertemporals and with the large lateral extrascapulars. Maxillaries long, underlying with their posterior ends the anterior ends of the quadratojugals, and attached in front to special processes of the vomers. . . . Palate extensively ossified, with very large entopterygoids meeting in a median suture, large vomers, and tooth-bearing dermopalatines and ectopterygoids. . . . Lower jaw with large supraangulo-angulars and prearticulars.

Lateral line system, at least for the greater part, enclosed in the dermal bones in canals, connected with the surface by primary tubes and pores. A true jugal canal in the jugal and squamosal.

External nares situated on the ventral surface of the skull, between the maxillaries and the tooth-bearing parts of the rostro-premaxillaries. Palate with anterior palatal vacuity and very narrow interpterygoid vacuities.

In discussing the Ichthyostegidae, Säve-Söderberg makes the following points:

He shows the ventral position of the external nares to be inherited by citing two indeterminate Crossopterygians from Spitzbergen, described by Stensio, which have two external narial openings on each side, of which the posterior one of each pair, very low on the side of the snout, is "quite clearly" the external naris of the Ichthyostegids.

Ichthyostegids have lost the cartilaginous portion in the middle of the skull and so the movability of the skull in a vertical direction. Studies by Stensio show that the divided cranium of the Crossopterygians is not primitive but that a solid, osseous cranium most probably is.

Ichthyostegids, in contrast to later Stegocephalians, have an unpaired parieto-extrascapular; an unpaired rostro-interrostral; an anterior antorbital; at least in certain forms, an independent preopercular; an enclosed lateral line system, not seen in later Stegocephalians.

Ichthyostegids *resemble* Carboniferous Stegocephalians: in the broad pterygoids meeting anteriorly in a suture; in the narrow interpterygoid vacuities; in possessing independent, tooth-bearing palatines and ectopterygoids; in vomers large and tooth-bearing as in Loxommids; in the size and shape of the internal nares and anterior palatal vacuities like those of certain Loxommidae. To these may be added the long maxillaries, anteriorly broadened nasals, narrow frontals, broad parietals, the shape and extent of the jugals, squamosals, and quadratojugals, as common possessions.

Ichthyostegids *differ from* Carboniferous Stegocephalians in the presence of two rows of teeth in the mandible; teeth in upper jaw of the same size as palatal teeth, relatively larger than the teeth of

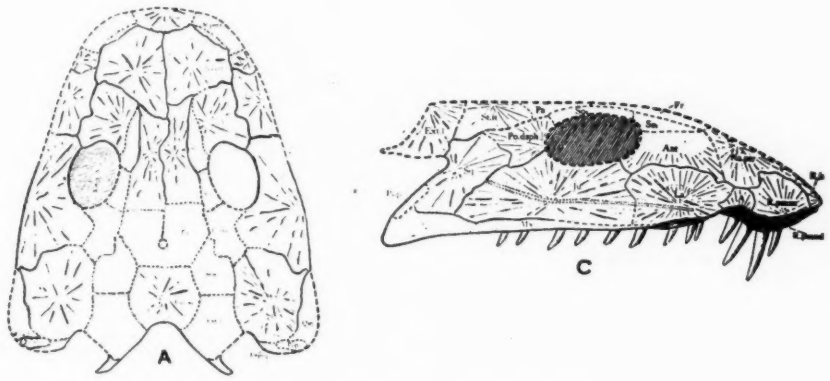


FIG. 178. *Ichthyostega*. Säve-Söderberg.

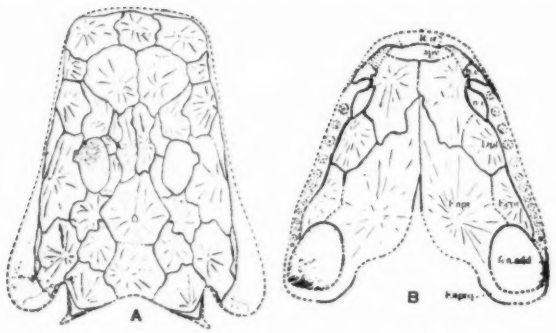


FIG. 179. *Ichthyostega*. Säve-Söderberg.

Embolomeri, and smaller than the palatine tusks of the Embolomeri; the anterior antorbital is homologous with the septomaxillary of later Stegocephalia; the septomaxillary is smooth in Permian Stegocephalians but is sculptured in Carboniferous Embolomerids and in *Orthosauriscus* (*Orthosaurus*) and *Baphetes*.

Certain Embolomeri have primitive characters inherited directly from fish ancestors not present in Ichthyostegids, as "a loose (ligamentous) mesial attachment of the squamosal to the supratemporal and intertemporal"; the "deep otic notch, wholly separating the small lateral extrascapular (tabular) from the squamosal, and the existence of free intertemporals or dermosphenotics (Loxomma)." In Ichthyostegids the attachment was by suture, primitive or secondarily acquired.

LIST SHOWING THE CLASSIFICATION, GEOLOGICAL HORIZON, AND LOCATION OF THE DETERMINABLE ICHTHYOSTEGALIA

Ichthyostegidae

Ichthyostega, Upper Devonian, of Ymer Island, East Greenland.

Ichthyostegopsis, Upper Devonian, of Ymer Island, East Greenland.

Ichthyostega (fig. 178*A*, *C*, 179*A*, *B*, 180*C*) has the characters:[14]

9. Skull long, at least not broad; lachrymal and jugal meeting anterior to the anterior border of the orbit; parietals only partially separated by suture which lies anterior to the parietal foramen.
10. Orbits small, near the midline, largely in the posterior half of the skull.
12. Nares. Internal nares entirely anterior to the anterior border of the orbit.
13. Lachrymal touching neither orbit nor naris.
14. Cornua formed by the tabular, well developed.
15. Intertemporal absent.
16. Otic notch present.

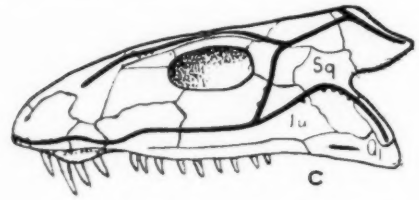


FIG. 180. *Ichthyostega*. Bystrow.

[14] The author has translated Säve-Söderberg's terminology into that in common use, to the best of his ability.

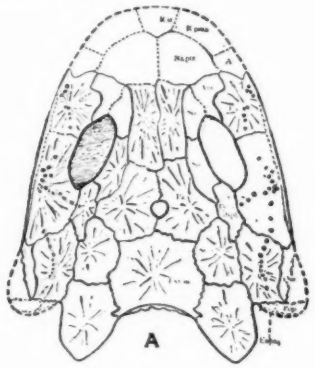


FIG. 181. *Ichthyostegopsis*. Säve-Söderberg.

Ichthyostegopsis (fig. 181*A*, 182*C*, 183*C*) has the characters:

9. Skull shorter and broader than in *Ichthyostega*, very high; parietals and frontals separated by suture.
10. Orbits large, round, lateral, largely in the anterior half of the skull.
12. Nares. Internal nares below anterior portion of the orbit.
13. Lachrymal extends from orbit to naris.

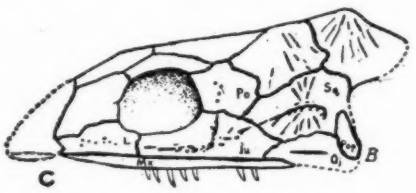


FIG. 182. *Ichthyostegopsis*. Bystrow.

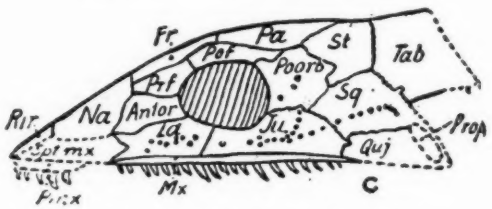


FIG. 183. *Ichthyostegopsis*. Bystrow.

14. Cornua formed by tabular, strongly developed.
15. Intertemporal absent.
16. Otic notch present.

SEYMOURIAMORPHA

The recently published detailed account of *Kotlassia prima Amalitzky*, by Bystrow, 1944, with the earlier description of *Seymouria baylorensis* Broili, by White, 1939, permits a good understanding of these forms and verification of the reality of the group Seymouriamorpha suggested by Watson, 1917. It is in a way fortunate that these two studies were made independently by competent workers without reference to each other's results. *Kotlassia* was known only from imperfectly prepared material at the time of White's work, and Bystrow was unaware of White's work, because of disturbed conditions, when he prepared and described the material upon which Amalitzky based his *Kotlassia prima* and *secunda*. Because of the independence of the work, the mutual verification of observations has added significance.

From the time of the first description of *Seymouria* by Broili in 1904, its unique character and uncertain systematic position has been evident. It has been referred to the reptilian Order Cotylosauria by Abel, Broili, Case, Hay, Huene, Nopsca, Pearson, Romer, White, and Williston, and to the amphibian Order Stegocephalia by Broom, Bystrow, Smith-Woodward, and Sushkin. Hartmann-Weinberg, 1929, was unable to arrive at a decision as to its position.

Watson, 1917, placed it in an independent Order Seymouriamorpha, and Nopsca, 1928, suggested a sub-order Seymouriamorphoidea. Hay, 1930, proposed a sub-order Conodectiformes with the family Conodectidae to replace Seymouriamorpha and Seymouridae, procedure which is strictly in accordance with the rules of nomenclature as *Conodectes* is an earlier name for *Seymouria*. The name *Seymouria*, however, has become so thoroughly entrenched in the literature that it is desirable to adopt Watson's expedient for retaining it. In 1917 he said, "As Cope's description of *Conodectes* is quite insufficient for recognition of the skull, and *Seymouria* is a name universally known, I propose to regard *Conodectes* as a *nomen nudum* and relegate it to the synonomy." This proposal has been followed by all recent writers.

From the first it has been recognized that the Seymouriamorpha contained a puzzling association of amphibian and reptilian characters. Watson, 1919, repeatedly commented on this. On page 292 he says that the characters of *Seymouria* are a mosaic of those peculiar to the Amphibia and Reptilia, with few if any indicating a transition from one to the other. On page 299 he says there is a

> strange mosaic of characters derived without change from the Embolomerous Labyrinthodonts with common reptilian characters making a distinct advance over an amphibian structure.

On page 300,

> The curious way in which the structure of *Seymouria* is built up of perfectly well developed amphibian characters and equally decisive reptilian features, those of intermediate type being very rare, affords a magnificent example of the way in which the evolution of the great groups may have taken place by the rapid change of all the definite morphological entities of which it may be regarded as made up, the changes occurring quite independently and over a considerable time, the passage from the structure of the more primitive to the advanced group being quite gradual when viewed as a whole, but when further considered and analysed found to depend on a rapid evolution of separate regions apparently independent of each other.

It is this association of distinctive characters which has caused the difference of opinion among workers, as each has given more or less weight to the features which appealed to him.

Watson's (1919) description of his Order Seymouriamorpha is:

> Cotylosaurs with a skull resembling in nearly all known details that of the Anthracosauridae. Otic notches small, quadrate inclined backward. Tabulars and dermo-supra-occipitals on the skull roof, but with occipital flanges. Pro-otic reaching the skull roof. Inner ear widely open to the cranial cavity in the lateral wall of the cranium. Vertebrae with very heavy and expanded arches and very large intercentra.
>
> Limbs very primitive, like those of the Rhachitomous amphibian *Eryops* in many features.

Nopsca's definition of the Seymouriamorpha and his Seymouriamorphoidea is:

> "embolomerous" imperforate palate, strong otic notch, numerous skull bones, stegocephalian-like mandible, no cleithrum, clavicles and episternum sculptured, one sacral vertebra, ribs dilated, tail moderately long.

List Showing the Classification, Geological Horizon, and Location of the Determinable Seymouriamorpha

Seymouriamorphidae (Conodectidae)

Seymouria, Lower Permian, Clear Fork, of Texas, U.S.A.

Kotlassia, Upper Permian, of North Dwina River, Russia.

Solenodonsaurus, Uppermost Stephanian, of Nyran, Czechoslovakia.

The family Seymouridae was proposed by Williston (1911) without characterization but with the remark,

> The relationships of *Seymouria* are, on the one hand, closest with *Limnoscelis*, on the other hand with *Labidosaurus*, but differing so markedly from both as to merit a co-ordinate independent position for the genus, which I prefer to call of family value—the Seymouridae.

This leaves us to infer that the distinctively amphibian features noted by Williston are characteristic of the family.

The definition of the family by Smith-Woodward (1932) is:

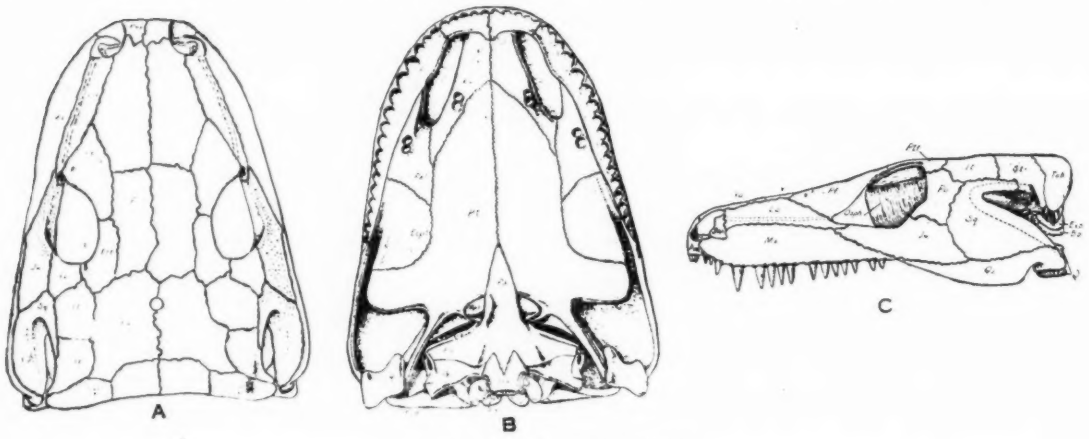


FIG. 184. *Seymouria*. White.

Skull triangular, with large oval orbits in hinder half. Occipital condyle single. Tabular and postparietal bones with occipital flanges. Pleurocentra relatively small. Clavicles expanded on ventral surface.

The sub-order Conodectiformes and the family Conodectidae proposed by Hay, 1930, were not defined. It is evident that he intended to change the names only in the interest of legality, and leave the definitions as previously given.

Seymouria (fig. 184*A*, *B*, *C*), with its synonym *Desmospondylus* and the unacceptable name *Conodectes*, has the following characters:

1. Body stout, not elongate.
2. Tail long as body; vertically expanded; chevrons and neural spines well developed.
3. Limbs stout short; carpus and tarsus ossified; entepicondylar foramen present in humerus.
4. Girdles Cotylosaur-like; clavicles and interclavicle expanded proximally, little or no sculpture; cleithrum present.
5. Vertebrae. 24 presacrals (23 according to Watson and Williston); neural arch and spines Cotylosaur-like; intercentra good sized or large; centra complete, notochordal.
6. Ribs double headed; cervical ribs expanded distally; thoracic ribs slender, curved, not elongate.
7. Sculpture reticulate, faint on skull and thoracic girdle.
8. Scutes absent.
9. Skull longer than broad, relatively high posteriorly; suggestion of sensory grooves on borders of orbits and otic notches; septomaxillary present; squamosal forms part of the upper edge of the otic notch; basioccipital present; condyle small, single, tripartite, concave; dermosupraoccipital short, broad; interpterygoid vacuities absent; anterior rami of pterygoid broad, meeting in midline anteriorly; basipterygoid processes of the basisphenoid articulate movably with the pterygoid; parasphenoid small, anterior process and body small, a small pointed posterior process; epipterygoid small or absent; supraoccipital cartilaginous (ossified in *Conodectes* according to Watson).
10. Orbits at midlength of the skull, lateral, oval, outer edge straight and with a notch at the anterior inferior corner.
11. Teeth. Tusks on prevomers and palatines, denticles on pterygoids and ectopterygoid; teeth of jaws simple cones with slightly infolded dentine.
12. Nares. External nares terminal, not widely separated. Internal nares elongate, separated.
13. Lachrymal touches orbit and naris.
14. Cornua absent; tabular cut off from otic notch almost completely by supratemporal.
15. Intertemporal present.
16. Otic notch deeply incised, faces laterally; a large tympanic membrane indicated.

The genus *Kotlassia* (fig. 185*A*, *B*) is placed by nearly all in the family Seymouridae; Romer (1933) suggests the family Kotlassidae but without definition.

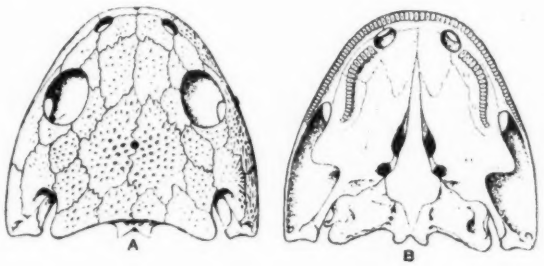


FIG. 185. *Kotlassia*. Bystrow.

Kotlassia, with its synonym *Karpinskosaurus*, has the characters:

1. Body elongate, narrow.
2. Tail long as body, vertically expanded; chevrons and neural spines well developed.
3. Limbs stout, short; carpus and tarsus ossified; no entepicondylar foramen in the humerus.
4. Girdles Cotylosaur-like; clavicles and interclavicle expanded distally, with strong sculpture.
5. Vertebrae. 26 presacrals; neural arch and spine Cotylosaur-like; intercentra good sized; centra complete, notochordal.
6. Ribs double headed; cervical ribs expanded distally; thoracic ribs long, slender, curved.
7. Sculpture reticulate, well marked in skull, clavicles and interclavicle.
8. Scutes. A dorsal armor of several rows of plates with a peculiar sculpture and a long, narrow keel on the ventral surface of each plate of the median row.
9. Skull short, wide, not elevated posteriorly; sensory grooves absent; septomaxillary absent; squamosal takes no part in the upper edge of the otic notch; basioccipital present; condyle single, concave, tripartite; dermosupraoccipital longer than broad; interpterygoid vacuities small; anterior rami of the pterygoids broad, not meeting in the median line anteriorly; basipterygoid processes of the basisphenoid movably articulated with the pterygoid; parasphenoid long, body small, anterior process long and slender, articulates with prevomers; a narrow posterior process; epipterygoid absent (?); supraoccipital cartilaginous.
10. Orbits in anterior half of the skull, oval, moderate size, lateral.
11. Teeth. No teeth on prevomer; a row on palatine and ectopterygoid paralleling the maxillary row; teeth of jaws conical, slightly recurved, oval in section at base; dentine infolded.
12. Nares. External nares nearly terminal, separated. Internal nares oval, small, separated.
13. Lachrymal touches both orbit and naris.
14. Cornua well developed.
15. Intertemporal present.
16. Otic notch deep.

Broili in 1924 erected the family Solenodonsauridae, characterized by the slender teeth recurved at the apex and with a longitudinal groove on the outer side, and by the triangular interclavicle without a posterior prolongation. Its single genus is generally placed in the Seymouridae.

Solenodonsaurus (fig. 186*A*) was founded by Broili, 1924, on a specimen previously identified by him as *Cochleosaurus*, and its counterpart later found in the museum of the University of Berlin. The specimens are from the Upper Carboniferous of Nyran. The characters as given by Broili and Pearson, 1924, are:

1. Body short, rounded.
3. Limbs. A large foramen entepicondylum.
4. Girdles. Clavicles and interclavicle slightly sculptured.
5. Vertebrae Cotylosaur-like.
6. Ribs single-headed, curved.
7. Sculpture of light pits and radiating ridges.
8. Scutes on venter, short, spindle-shaped.
9. Skull elongate, triangular; parietal foramen small or absent; no spoon-shaped extension of the dermosupraoccipital.
10. Orbits in midlength of skull, oval, separated but not lateral.
11. Teeth of jaws simple cones, slender, apex recurved; laterally compressed with a groove on the outer side; no infolding of the dentine.
12. Nares. External nares lateral.
13. Lachrymal touches both orbit and naris.
14. Cornua small formed by tabular.
15. Intertemporal present (?), unknown.
16. Otic notch small ("probably present"—Broili).

According to Pearson, 1924, *Solenodonosaurus* differs from *Seymouria* in having single-headed ribs, more prominent neural spines, teeth without infolding of the dentine. Pearson remarks that "teeth, however, are never a character of much systematic value," a point of view that would not be universally accepted.

Watson in 1914 described a femur from the Lower Carboniferous of Scotland which he regarded as reptilian and said that it was much like that of *Seymouria*. Should a skeleton of this form be found it might add one more genus to the Seymouriamorpha.

From the discussion given it is obvious that there is a general concensus of opinion on three points:

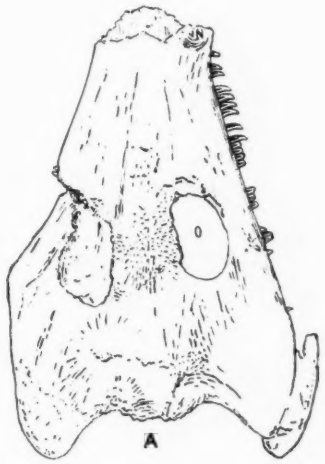


FIG. 186. *Solenodonsaurus*. Broili.

1. The Seymouriamorpha, consisting of the three genera, *Seymouria*, *Kotlassia*, and *Solenodonsaurus*, constitute at present a distinct group of which the nearest relationship, amphibian or reptilian, is not a matter of common agreement.

2. The group retains many characters stemming directly from the early Embolomeri although it has been involved in the great non-adaptive trend culminating in the possession of true reptilian vertebrae.

3. The group has maintained an independent course from the time of its inception, retaining among other early characters a single, tripartite occipital condyle. This frees us from the dilemma of explaining a change from a single condyle to a double one and a return to a single condyle in the reptiles.

The three genera are easily distinguished and the three families proposed may eventually be recognized as valid. All show the striking mixture of ancient and advanced characters which are the peculiarity of the group. The ancient characters are:

7. Sculpture deep in *Kotlassia* (*K*), faint in *Seymouria* (*Se*) and *Solenodonsaurus* (*So*).
9. Sensory grooves present (*Se*); interpterygoid vacuities small (*K*) or absent (*Se* and *So* ?); parasphenoid small (*Se*, *K*, *So*?); occipital condyle tripartite, single (*Se*, *K*, and probably *So*).
11. Teeth. Dentine infolded (*Se*, *K*, and *So*?).
13. Lachrymal extends from orbit to naris (all).
15. Intertemporal present (*Se*, *K*, and *So*?).
16. Otic notch deep (*Se*, *K*, and *So* probably).

The advanced characters are:

3. Limbs stout, strong; carpus and tarsus ossified (all).
4. Girdles Cotylosaurian (all).
5. Vertebrae Cotylosaurian (all).
6. Ribs elongate, slender, curved (all); double headed (*Se* and *K*), single headed (*So*).
8. Scutes absent (*Se*, *K*), present (*So*).
14. Cornua absent (*Se*), small (*So*), well developed (*K*).

It is easily seen how the group might be referred to either the Reptilia, as White, or the Amphibia, as Bystrow, according as the worker gave weight to one or the other of the two groups of characters. Säve-Söderberg's suggestion of the fundamental difference between the Loxommids and the Anthracosaurids seems justified. The acceleration in the development of a reptilian axial skeleton may be explained by any one of several guesses, all unprovable and unprofitable, but if we recognize that no one of the workers interested in the group has been able to suggest a more dependable criterion, and adhere to the long established and well famed classification based upon the structure of the vertebrae, we must admit the dominantly reptilian nature of the Seymouriamorpha.

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